Pan-Temperate Floral Elements on the African High Mountains

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INTRODUCTION

Biogeography aims to explain why particular taxa have certain geographical distributions (De Candolle 1880; Lomolino et al. 2006). Why are beeches (*Fagus spp.*) found exclusively in the Northern Hemisphere and southern beeches (*Nothofagus spp*.) exclusively in the Southern Hemisphere? Why are there lions in Africa, but Tigers in Asia? This is closely linked to the question of speciation, so why are there only ten species of beeches but 35 of southern beeches? Why only one giraffe species (*Giraffa camelopardalis)* but seventeen species of gazelles (*Gazella spp.)*?

Islands have often been used to test biogeographic hypothesis or to investigate what is driving speciation (Grant 1996). Oceanic islands, e.g. Hawai'i or the Galapagos islands, which are typically of volcanic origin or formed by corals, have never been connected to a continent. This means that vicariance (i.e., fragmentation of widespread ancestors by isolating events, such as the breakup of continents) can be ruled out as an explanation of their species assemblage.

One of the most influential theories developed to explain species assemblage on such oceanic islands has been MacArthur and Wilsons (1967) theory of island biogeography. According to island biogeography theory, species assemblage is determined by the dynamic interaction between colonization and extinction depending on island area and distance to the mainland. However, until recently long-distant dispersal was still thought to be rather rare (Humphries and Parenti 1999; Cowie and Holland 2006; Lomolino et al. 2006). More recently it has been shown that long-distant dispersal is more common than expected and that establishment is often the limiting factor and not the frequency of dispersal (de Queiroz 2005; Levin 2006; Alsos et al. 2007; Heaney 2007).

That dispersal can occur over large distances means that recruitment of taxa can occur from many different source areas. For example the Cape flora has been shown to comprise of lineages which originated not only from Tropical Africa and Southern Africa but also from South America, North America, Eurasia, and Australasia (Galley and Linder 2006; Galley et al. 2007). Similarly far flung origins have been documented for the flora of Hawai'i (Wagner et al. 1990) and New Zealand (McGlone et al. 2001; Winkworth et al. 2005; McDowall 2008). Although geographically closer areas tend to contribute the highest proportion of species (Linder 1990; Eggens et al. 2007), more distant regions can have a profound importance especially when they have a similar climate (Smith and Cleef 1988).

Although island equilibrium theory does not take diversification into account, MacArthur and Wilson (1967) never denied the importance of speciation. Nevertheless, they stated that over time speciation might become more important than colonisation, especially on remote islands. Most plant and animal taxa on Hawai'i, for example, have been shown to have originated from a single colonisation event followed by extensive in

situ speciation (Baldwin and Sanderson 1998; Schluter 2000; Eggens et al. 2007). The cause of diversification in these cases has mostly been ascribed to adaptation driven by competition (Darwin 1859; Osborn 1902; Lack 1947; Givnish 2000; Schluter 2000). Where this has resulted in high numbers of species, for example in drosophilae flies (CITATION) or the Hawai'ian silverswords (Baldwin and Sanderson 1998; Barrier et al. 1999), this is referred to as adaptive radiation. However, the role of colonisations and in situ speciation are still much debated.

Investigation of the frequency of colonisation event and their directionality and revealing factors driving speciation is limited by the availability of phylogenetic hypotheses (Stebbins 1950; Grant 1981). The emergence of methods to infer phylogenetic hypotheses (Hennig 1966) and the increased availability of DNA sequence data have provided the means to reconstruct robust phylogenetic hypothesis based on independent characters. This in combination with the development of character optimisations on phylogenetic trees (Swofford and Maddison 1987) has allowed for a new set of comparative macro-evolutionary studies (Givnish and Sytsma 1997) that has had a great influence on the development of the field of biogeography.

The study of closely related species (i.e. sister species) can lead to the identification of factors which influence speciation. This approach however fails to reveal large-scale patterns due to the absence of repetition. The same is true both when investigating only single lineages and, on a different scale, when investigating only single islands. A number of authors have used a comparative approach across multiple lineages and regions and thereby identified factors other than allopatry which influence diversification. Amongst the most influential abiotic variables thus identified were area, elevation, isolation, colonisation/history and age (Juan et al. 2000; Allan et al. 2004; Price & Wagner, 2004; Parent & Crespi, 2006; Heaney, 2007; Ricklefs, 2007). One of the most debated factors potentially influencing diversification is diversity itself (Emerson & Kolm 2005). The idea of an environmentally-determined influence on diversification is less controversial (Schluter, 2000; Whittaker et al., 2007). Habitat heterogeneity has been used as a measure of the complexity of these environmental factors, because it refers to both the spatial variation and the structural diversity in the environment (Bazzaz, 1975; Schluter, 2000; Kassen et al., 2004). Some authors even suggest that habitat heterogeneity rather than area or elevation per se, is the most important predictor of diversification, since habitat heterogeneity usually increases with area size and elevation (Tews et al., 2004; Baldi, 2008).

Mountains, like islands, provide an excellent means for the study of evolutionary processes. Just as islands are isolated at sea level by a barrier of salt water, the upper regions of mountains are isolated one from other by, for mountain species, inhospitable surrounding lowlands (Brühl 1997; Cohen et al. 1997; Hedberg 1970; Menocal de 200). Therefore all lineages which are not derived from lowland species must have arrived on these 'sky-islands' by dispersal. The advantage of studying mountain or mountainous islands is that mountains have high levels of habitat heterogeneity, for the most part due

to rapid changes in edaphic and climatic factors along altitudinal gradients resulting in high rates of species turnover over short distances. This can result in mountain lineages with high levels of diversity (Hughes & Eastwood, 2006; Moore & Donoghue, 2007; Tkach et al., 2008).

In this thesis I have investigated the role of colonisation frequencies (chapter 1) and in situ diversification (chapter 2) in the African high mountains of Tropical and Southern Africa (fig.1 and 2). I have focused on plant elements from temperate areas around the world (i.e. pan-temperate plant elements) and have mainly concentrated on the three genera *Alchemilla* (Rosaceae, ladies mantle), *Carex* (Cyperaceae, segges) and *Ranunculus* (Ranunculaceae, buttercups). For this investigation it was necessary to obtain robust phylogenetic hypotheses. Although classical α-taxonomy is usually based on careful investigation of morphology, traditional groupings of species do not necessarily reflect phylogenetic relationships (see chapter 3 for *Alchemilla* as an example of this).

It is important to ensure that any shortfall in the accuracy of the taxonomy of a group does not impact evolutionary interpretations that are made. Incorrect taxonomy can lead to too sparse sampling which can affect the reconstruction of characters or lead to erroneous estimations of evolutionary diversity. Robust phylogenetic reconstructions are ideally based on complete taxon sampling, which is unfortunately rarely archived. Under certain circumstances, morphology can be used to place species for which sequence data is not available (Hardy and Linder 2007). Unfortunately, African taxa are generally understudied and even a basic understanding of morphological diversity within and between species is often lacking. I therefore revised the available literature and studied a large number of herbarium specimens in *Carex* (chapter 4) to be able to make more precise estimations of species numbers in the different African mountain clades of the genus (see chapter 2).

In the following four chapters of this thesis I have used a wide array of classical taxonomic, systematic and biogeographic tools to investigate the importance of colonisation and speciation in African high mountains.

In **chapter 1** I investigate together with Peter Linder how often the pan-temperate elements *Alchemilla* (Rosaceae), *Carex (Cyperaceae)* and *Ranunculus* (Ranunculaceae) have colonised the African high mountains. I investigated this by reconstructing hypotheses of their phylogenetic relationships based on DNA sequence data and used these to test both the monophyly of the African mountain clades, and the monophyly of these clades plus at least one additional sister species from outside this area, using parametric and non-parametric bootstrapping methods. We are able to demonstrate that *Alchemilla* arrived only twice (see also chapter 3), *Carex* has colonised the African high mountains at least twelve times, while *Ranunculus* arrived and established itself at least four to six times. We further investigated the source areas of these colonisations and can show that all three groups are of temperate Northern Hemisphere, i.e. Holarctic, origin.


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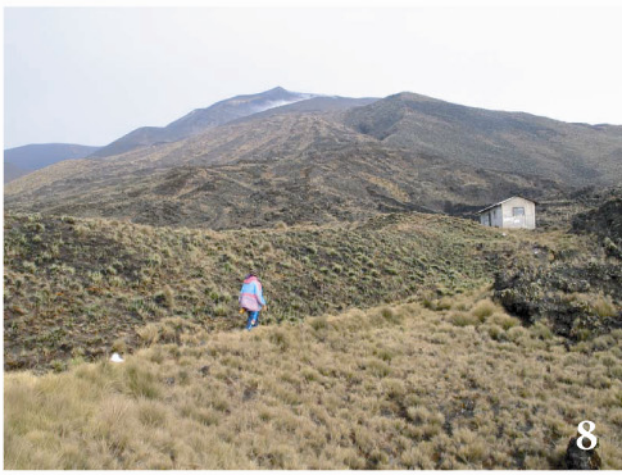
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The different lineages which have colonised the African high mountains have undergone varying amounts of in situ speciation. In **chapter 2** I investigated together with Peter Linder what have been the main factors influencing this diversification. We employ the novel approach of investigating the repetitive recruitments of *Carex* and *Ranunculus* into the temperate climate zones of the African mountains. We tested the relationship between both clade size and the relative ages of clades and several important (a)biotic factors such as distribution range, isolation/distance from ancestral area, altitudinal range, number of vegetation zones, number of habitat types, light requirement, water availability and habitat heterogeneity, using regression analysis under generalized linear models. We can show that clade size is dependant on a combined model including age, distribution and habitat as represented by water availability or altitudinal parameters.

Alchemilla in Africa consists of only two clades (one forming the monospecific Aphanes-clade and one leading to the great diversity of African *Alchemilla* species in the Afromilla-clade). This was the unexpected result of analyses of *Alchemilla, Aphanes* and *Lachemilla* described in **chapter 3.** This has been published together with a number of other authors, who have contributed plant material (Katya Romoleroux), sequence data (of eight species from Magnus Lundberg and twenty from Christian Bräuchler) or input on the manuscript (especially Torsten Eriksson and Christian Bräuchler, as well as Günther Heubl). We suggest treating *Alchemilla, Aphanes* and *Lachemilla* as a single genus *Alchemilla*, based on their monophyly, the lack of evident morphological characters for the identification and description of the Afromilla-clade at the rank of genus (without which *Alchemilla* from Eurasia would be rendered paraphyletic) and in order to maintain nomenclatural stability.

Figure 1: Illustration of different African high mountains: **1**. Ethiopia, Bale Mts., Sanetti Plateau, c. 4'000 m, *Lobelia rynchopetalum* (Campanulaceae) with Desalegn Chala, Cyril Guibert and A. Muthama Muasya (from left to right); **2**. Uganda, Rwenzori Mts., Lower Bigo Bog, c. 3'4000 m, *Lobelia bequaertii* (Campanulaceae) with H. Peter Linder (left) and Sam Sibianumya (right); **3**. Kenya/Uganda, Mt. Elgon, inside the caldera, c. 3'800 m, *Dendrosenecio elgonenesis* (Asteraceae), *Alchemilla argyrophylla* (Rosaceae) and *Carex runssoroensis* (Cyperaceae); **4**. Kenya, Aberdare Mts., Oldonyo Lesattima, m, c. 3'700 m, *Dendrosenecio keniodendron* (Asteraceae) and *Festuca sp.* (Poaceae) Eric Knox; **5**. South Africa, Drakensberg Mts., Bushmans Nek area, c. 2'500m; **6**. Cameroon, Mt. Cameroon, c. 3'900 m; **7**. Malwai, Nyika Plateau, c. 2400m; **8**. Kenya, Aberdare Mts., view on *Hagenia abyssinica* (Rosaceae)- forest, flanked by *Erica sp.* (Ericaceae), c. 3'400 m (photos B. Gehrke 2004-2007)

The last chapter, **chapter 4**, is an α-taxonomical treatment: a synopsis of *Carex* in Tropical and Southern Africa and Madagascar. It provides a key, synonymy, habitat descriptions, and distributions for 84 species and an additional five infraspecific taxa. The genus *Carex* (Cyperaceae; Cariceae) currently comprises c. 1600-2000 species (Kubitzki 2004), making it one of the largest genera of vascular plants. It has an almost worldwide distribution with highest species numbers in Eastern Asia and North America. The last comprehensive treatment of *Carex* in Africa dates back to Kükenthal's monograph of the subtribe Cariceae in 1909. Subsequent descriptions of new taxa and regional taxonomic treatments have led to inconsistencies in species delimitations and confusion regarding the identification of specimens and correct application of names. The synopsis presented here is intended to summarise the scattered literature on *Carex* in Africa, including notes on the taxonomic status of species as appropriate and a comprehensive key for all species of *Carex* from Tropical and Southern Africa and Madagascar. It is also the basis of the estimation of species numbers in chapter 2.

CHAPTER 1:

The scramble for Africa: pan-temperate elements on the African high mountains

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ABSTRACT

The composition of isolated floras has long been thought to be the result of relatively rare long-distance dispersal events. However, it has recently become apparent that the recruitment of lineages may be relatively easy and that many dispersal events from distant but suitable habitats have occurred, even at an infraspecific level. The evolution of the flora on the high mountains of Africa has been attributed to the recruitment of taxa not only from the African lowland flora or the Cape Floristic Region but to a large extent from other areas with temperate climates. We used the species rich, pan-temperate genera *Carex*, *Ranunculus* and *Alchemilla* to explore patterns in the number of recruitment events and region of origin. Molecular phylogenetic analyses, parametric bootstrapping and ancestral area optimisations under parsimony indicate that there have been a high number of colonisation events of *Carex* and *Ranunculus* into Africa but only two introductions of *Alchemilla*. Most of the colonisation events have been derived from Holarctic ancestors. Backward dispersal out of Africa seems to be extremely rare. Thus, repeated colonisation from the Northern Hemisphere in combination with in situ radiation has played an important role in the composition of the flora of African high mountains.

Keywords: Biogeography; test of monophyly; dispersal; colonisation; Afroalpine; island floras

INTRODUCTION

Isolated floras such as on Hawai'i, the Galápagos and the Macaronesian Islands probably evolved from a few long-distance dispersal events (Cowie and Holland 2006; Lomolino et al. 2006). However, recent evidence indicates that this may not be the general pattern, and that long distance dispersal may be more frequent than previously thought (de Queiroz 2005; Heaney 2007; Levin 2006). Alsos et al. (2007) even suggested that plant recruitment to the isolated Arctic island Svalbard is limited by establishment and not by dispersal. They showed additionally that Svalbard was colonised from various source areas. This importance of geographically widespread recruitment areas in the assembly of floras was also demonstrated for the Cape flora, where lineages were sourced from South America, North America, Eurasia, Africa, and Australasia (Galley and Linder 2006). Similarly far flung source areas have been documented for the flora of Hawai'i (Wagner et al. 1990) and New Zealand (McDowall 2008; McGlone et al. 2001; Winkworth et al. 2005).

The cool-adapted flora of the high mountains in tropical and southern Africa (Figure 1) is sharply distinct from the lowland tropical flora. Whereas the tropical flora is mainly composed of pan-African genera belonging to Takhtajan's African Subkingdom (Takhtajan 1986), the mountain flora contains elements derived from the Cape Floristic Region, the Mediterranean, the Northern Hemispheric and the Southern Hemispheric temperate regions, in addition to some lineages derived from the lowland tropical flora (Engler (1892; 1904); Hedberg (1961; 1965; 1970). These scattered high mountains and mountain ranges can, by analogy to oceanic islands, be referred to as "sky islands". Their cool-adapted floras have always been well separated from each other, and also from extra-African areas with similar climatic conditions and vegetation types, by large expanses of much drier surrounding lowland habitats (Brühl 1997; Cohen et al. 1997; Hedberg 1970; Menocal de 2004). There have only been few biogeographical analyses of taxa from the African mountain flora. A number of groups from the Cape Floristic element, for example, were shown to be derived from several unidirectional colonisation events, which entered the tropical mountains from the south (Galley et al. 2007). Most of these colonisations from the Cape Floristic Region resulted in small radiations in the tropical mountains. Other species (e.g. *Arabis alpina, Lychnis* and *Cardamine*) have been shown to have been derived from colonisations from the north (Carlsen et al. 2007; Koch et al. 2006; Popp et al. 2008). However, patterns of recruitment of the pan-temperate element, which constitutes the largest component of this flora (Hedberg 1961), is not known.

Here we use three typical pan-temperate genera (*Carex*, *Ranunculus* and *Alchemilla*) to investigate the patterns in the recruitment of this floral element. Considering the enormous distances between the African mountains to other locations of the pan-temperate flora, we ask whether the pan-temperate recruitment was by a minimal number of dispersals (comparable to the situation in Hawai'i) or numerous dispersals (comparable to the Svalbard model).

Secondly, we investigate whether the pan-temperate taxa are recruited from all areas where they occur (as seems to be the normal situation), or from a limited subset of regions. Finally, we investigate how common reverse colonisation is (e.g. out of Africa).

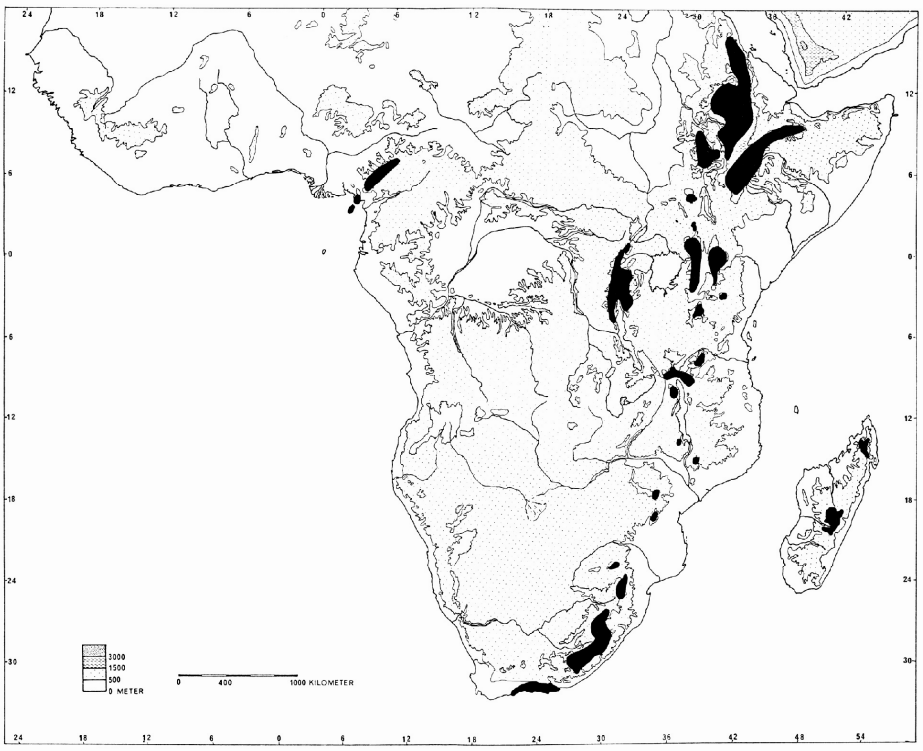

Figure 1: Distribution of the high mountain areas in Tropical and Southern Africa and Madagascar.

MATERIALS AND METHODS

Taxon sampling

We focused on the more or less globally distributed, mostly cool-climate (i.e. pan-temperate) genera *Carex*, *Ranunculus* and *Alchemilla*, which are species rich, geographically widespread and have a wide altitudinal range in the African high mountain flora. We refer to the African high mountain flora as species found above 2300m in Tropical Africa, 1300m in Southern Africa outside the Cape Floristic Region as well as on Madagascar above 2000m. We included as many taxa as possible from outside the African high mountains to improve the reliability of the monophyly test (Appendix 1 and Appendix 2). Where possible, multiple accessions for each species from geographically distant locations in Africa were included. This was done to test the monophyly of the species and to detect problems arising from introgression and paralogues that are commonly found in highly polyploid groups such as *Carex, Ranunculus* and *Alchemilla*.

The genus *Carex* (or the tribe Cariceae, if the endemic African genus *Schoenoxiphium* is included) is, with 1600-2000 species, the largest clade in the Cyperaceae. The subgenus *Indocarex* comprises mainly tropical or subtropical *Carex* species, the African distribution of which is largely outside the African high mountain regions. Taxa of *Indocarex* were therefore only included to test the affiliation of individual species to the subgenus, and were excluded from the biogeographical inferences made.
There is no recent revision of African *Carex*, and consequently the number of species can only be estimated: most likely there are around 40 species, with an additional 40 *Indocarex* species and 15-25 species of *Schoenoxiphium*.
Due to the availability of data from a number of recent molecular phylogenetic studies of *Carex* (Hendrichs et al. 2004a; Hendrichs et al. 2004b; Roalson et al. 2001; Roalson and Friar 2004; Starr et al. 2004; Yen and Olmstead 2000) we were able to include over 600 accessions representing ca. 550 species in our analyses. *Cariceae* from the high African mountains are represented by 82 accessions of 43 taxa which accounts for 78% of all taxa from the high mountains in Africa in the subtribe. An additional 18 accessions represent 14 taxa of *Indocarex*. All other sequences were downloaded from NCBI GenBank (Appendix 1). The total matrix of 602 accessions included 554 sequences of nuclear ITS and 365 of the chloroplast marker *trn*L-*trn*F.

Ranunculus (the buttercups) is, with ca. 600 species, the largest genus within Ranunculaceae (Tamura 1995). Buttercups are cosmopolitan. Most species occur in temperate to arctic/subantarctic regions (Paun et al. 2005), in terrestrial or aquatic habitats, and from the coast to alpine vegetation. In the tropics they are restricted to tropic-alpine or high mountain habitats. Two hundred and thirty *Ranunculus* species were included in the analyses, representing material from all continents and including representatives of all subgenera and sections (Hörandl et al. 2005; Paun et al. 2005). Of the 232 accessions of *Ranunculus* analysed, 27 represent 16 of the 20 African taxa (80%), missing only four species endemic to Ethiopia and the Rwenzori Mountains. New sequences were generated for nuclear ITS and a chloroplast marker (*mat*K) (Appendix 2) and all other accessions were downloaded from NCBI GenBank.

The genus *Alchemilla* has a global distribution (Fröhner 1995). According to Gehrke et al. (2008) the African members form two clades, referred to informally as 'the Afromilla clade' and the 'Aphanes clade'. The Afromilla clade is endemic to tropical Africa (ca. 20-25 species), southern Africa (4-6 species) and Madagascar (6 endemic species). Most herbaceous *Alchemilla* species in Africa are widespread, whereas many woody taxa are endemic to single mountains (i.e. Rwenzori) or montane regions (Ethiopia or Tropical East Africa). In addition to the Afromilla clade a single species of *Alchemilla* subgenus *Aphanes* occurs in Ethiopia (*A. bachiti*). However, it is rare and we were not able to sample it for this study. Sequence alignment of nuclear ITS and chloroplast *trn*L-*trn*F, as well as the molecular phylogenetic reconstruction, were as described in Gehrke et al. (2008).

DNA extraction, PCR amplification and sequencing

Leaf material was pulverised using a Regget Machine and DNA was extracted using DNeasy extraction kit (Qiagen). Polymerase chain reactions (PCR) were performed in 25 µl reactions (1 x PCR buffer, with 2.5 mM $MgCl_2$, 0.25 mM dNTPs, 1.6 µM primers and 1 unit of Taq polymerase (Sigma-Aldrich, USA) in a Biometra Thermocycler TGradient (Biometra, Göttingen, Germany). Either 2µl BSA or 1µl BSA and 1µl EDTA was added to each reaction. The ITS1-5.8S-ITS2 region and the *trnL-F* intergenic spacer together with the *trnL* intron were amplified and sequenced using Primers ITS-I and ITS4 (Urbatsch et al. 2000) and *trn*LF-c and *trn*LF-f (Taberlet et al. 1991) for *Carex*.

For *Ranunculus* the protocol of Hörandl et al. (2005) for the ITS and matK-region was used. PCR products were purified using DNA band purification kit (Amersham Biosciences, Otelfingen, Switzerland). Cycle sequencing was carried out on an ABI Prism, LA, USA 3100 Genetic Analyzer (Applied Biosciences, Foster City, CA, USA) using BigDye terminator version 3.1. Forward and reverse strand sequences were edited using Sequencer 4.2. (Genecode) and aligned by hand using Sequence Alignment Editor v2.0 (Rambaut 2002).

Phylogenetic analyses

Simple Indel Coding (Simmons and Ochoterena 2000) was performed by hand for *Cariceae* and using SeqState 1.32 for *Ranunculus* (Müller 2005), excluding ambiguous areas in the alignment. An initial analysis of *Cariceae* including all taxa for the ITS and *trn*LF separately using TNT with standard "new technology" settings (Goloboff et al. 2003) identified three clades of taxa corresponding to subgenera *Carex* (including *Indocarex*), *Vignea* and *Psyllophora,* with the latter including *Kobresia*, *Schoenoxiphium* and *Uncinia* sensu Kükenthal (1909) (Appendix 4). Subsequent parsimony analyses were performed on these three clades separately as well as on *Ranunculus*, using PAUP* version 4.0b10 (Swofford 2001), with heuristic search of 1000 replicates, random sequence addition, tree-bisection-reconnection (TBR) branch swapping, MULTREE on (keeping multiple, equally parsimonious trees), saving a maximum of 50 trees per replicate. Support was assessed using 1000 replicates of non-parametric bootstrap analysis using the same settings as in the heuristic search. The nuclear and plastid loci of *Cariceae* and *Ranunculus* were analysed separately, and since no conflicting nodes received bootstrap support ≥70%, the loci were combined. The phylogenetic trees of *Alchemilla*, based on ITS and *trn*L-*trn*F data, were taken from Gehrke et al. (2008) and were constructed using the same methods as those for *Cariceae* and *Ranunculus*.

Bayesian analysis was performed as implemented in MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001). We identified the general time reversible (GTR) model with gamma distributed rates (G) and a proportion of invariable characters (I) as best fitting the sequence data of the individual loci in the *Cariceae* and *Ranunculus* matrices, using Modeltest v3.7 (Posada and Crandall 1998) applying the Akaike Information Criterion. The prior values for the number of parameters in the DNA substitution models were therefore

set to NST=6 + G + I. The dataset was partitioned into ITS and *trn*LF loci and parameter values of each varied independently. These settings were duplicated for t**wo** or three independent MCMC runs of each matrix (as below), with three heated and one cold chain each, sampling every 1000 generations from the cold chain.

In *Cariceae*, Bayesian analyses were carried out separately for each of the subgenus taxon sets with the combined data, and with the following number of generations and runs**:** *Psyllophora* taxon set, 2 x 2,000,000 generations; *Carex* subgenus *Vignea*, 3 x of 5,000,000 generations; for subgenus *Carex*, 2 x 10,000,000 generations. *Ranunculus* was analysed using two separate, independent runs of 5,000,000 generations. Convergence and sampling of model parameters was estimated using the program Tracer ver. 1.3 (Rambaut and Drummond 2005). Topologies sampled prior to convergence to the optimal mean log likelihood plateau were discarded as burn-in (2x3,000,000 generations for *Carex* subgenus *Carex*, 3x1,000,000 generations for *Carex* subgenus *Vignea* and 2x1,000,000 generations for *Carex* subgenus *Psyllophora,* 2x1,000,000 generations for *Ranunculus*) and clade posterior probabilities were computed from the remaining trees as a measure of node support.

Parametric bootstrapping as a test of monophyly

We determined the minimum number of colonisation events needed to constitute the African high mountain floras of the study groups, by locating the largest possible clades with an ancestral area in the high mountains of Tropical and Southern African. We used parametric bootstrapping (Huelsenbeck et al. 1996) to evaluate whether the monophyly of even larger, more inclusive clades is rejected by the data (which would reduce the number of colonisation events needed). We investigated whether the increase in tree length caused by constraining the monophyly of such groups of African taxa could be due to stochastic processes of sequence evolution. For details on parametric bootstrapping and the different constraints used see Appendix 4.

Ancestral area reconstruction

In order to locate the geographical origin of each African high mountain clade the distribution ranges of their ancestral nodes were reconstructed using unambiguous parsimony optimization as implemented in MESQUITE v. 2.0 (Maddison and Maddison 2006). We incorporated phylogenetic uncertainty by using all most parsimonious trees, summarising the resulting optimisations on the Adams consensus tree, one of the most parsimonious trees and the majority rule consensus. The Adams consensus was used because it is particularly useful for identifying common tree structure when one or more taxa have very different positions in the trees of the profile. The areas used were (1) African high mountains, (2) western temperate and boreal Eurasia, (3) eastern temperate and boreal Eurasia (4) the Mediterranean region including North Africa and Macaronesia, (5) North America, (6) South America and (7) Australasia. The Cape Floristic Region was not coded separately since none of the included taxa is only found in this area.

RESULTS

A summary of each clade of African high mountain taxa used in our analysis can be found in Table 1. For a more detailed description of these clades see Appendix 3. There were at least thirteen colonisation events into the African high mountains by *Carex* and four to six colonisation events by *Ranunculus* (Figure 2). Parametric bootstrapping confirmed the non-monophyly of the African high mountain clades, indicating that they have been derived from different non-African high mountain ancestors (Appendix 4). All African high mountain clades are nested within Northern Hemisphere clades. In some cases the closest related species could not be identified due to weak support values or incomplete taxon sampling (Appendix 5). In two cases dispersals out of the African high mountains could not be rejected, however no such event is supported (Appendix 3).

Table 1 African high mountain clades in molecular phylogenetic analysis of *Carex, Ranunculus* and *Alchemilla*. Bootstrap support values and Baysian clade credebilities of the monophyly of the clades in the combined analyses of ITS and *trn*LF are given. Bootstrap support values are indicated at the left and Baysian clade credebilities in brackets. Clades with higher support for one marker region are marked with an asterisk and the value given after the slash. Abbreviations for the parsimony ancestral area reconstructed are: E Eura.=eastern Eurasia, W. Eura.=western Eurasia, Med..=Mediterranean and Northern Africa, N-Am.= North America.

clade names	clade support:	reconstructed ancestral area
Carex* subg. *Carex		
Acutiformis-clade	66/89*(--)	N-Am./E.Eura.
Bequaertii-clade	99 (1.00)	W.Eura.
Cognata-clade	70 (--)	N-Am.
Johnstonii-clade	99 (1.00)	W.Eura
Madagascariens-clade is	58 (--)	N-Am.
Monotropa-clade	1 accession	W.Eura.
Simensis-clade	--/67* (0.93)	Med.
Carex* subg. *Vignea		
Conferta-clade	81/91*(0.99)	N-Am.
Glomerabilis-clade	97 (1.00)	W.Eura/Med.
Erythrorrhiza-clade	100 (--)	W.Eura./Med.
***Carex* subgenus *Primocarex* and other Cariceae**		
Monostachya-clade	100 (1.00)	N-Am.
Peregrina-clade	100 (1.00)	W.Eura.
Schoenoxiphium	-- (0.99)	W.Eura.
Ranunculus		
Meyeri-clade	1 accession	E.Eura.
Multifidus-clade	97/0.98	E.Eura.
Oreophytus-clade	-- (--)	E.Eura. (0-2)
Stagnalis-clade	67/1.00	Med.
Trichophyllus-clade	1 accession	W.Eura.
Volkensii-clade	86 (1.00)	E.Eura.
Alchemilla		
Afromilla-clade	100 (1.00)	E. Eur.?

Most of the colonisations appear to have derived from the Northern Hemisphere, mainly from temperate Eurasia (Appendix 6). Parsimony optimisations revealed four to eight colonisations of *Carex* from temperate Eurasia, one to three from the Mediterranean and four to five from North America. For *Ranunculus*, parsimony optimisations suggest five to six colonisations from temperate and boreal Eurasia and one from the Mediterranean, none from North America, and none from South America (Figure 3). *Alchemilla* (i.e. the Afromilla clade) was reconstructed as originating from eastern Eurasia (Appendix 6).

DISCUSSION

Multiple recruitments into the high mountains in Tropical and Southern African

We show that *Alchemilla, Carex* and *Ranunculus* colonised the high mountains of Africa several times. This pattern has also been reported for other temperate groups present in the African mountains such as *Myosotis*, *Swertia*, *Cardamine* and *Trifolium* (Bleeker et al. 2002; Carlsen et al. 2007; Chassot et al. 2001; Ellison et al. 2006; Winkworth et al. 2002a), as well as for clades centred in the Cape Floristic Region and which reach into the high African mountains, e.g. *Pentaschistis*, *Disa*, *Iridaceae* (Galley and Linder 2006). *Alchemilla, Carex* and *Ranunculus* show substantially fewer affiliations outside the African mountains than calculated by Hedberg (1965), who postulated that two thirds of all species have been derived from areas outside the African mountains. However, the numbers of dispersal events to 'islands' are usually underestimated, especially in the absence of species level phylogenies. This happens when all members of a taxon are assumed to be the result of a single colonisation event followed by *in situ* radiation (Grant 1996), as has been reported for most taxa of the Hawai'ian flora (Price and Wagner 2004). Additionally, the number of recruitments can be underestimated when the delimitation of taxa has been influenced by geographic distribution. This applies especially to large groups with extensive distribution areas across countries and continents. Categorising taxonomic units, such as species, as 'Cape' or 'Australasian' may also lead to an underestimation of the number of colonisation events, as it makes the implicit assumption that the current geographical range is the result of a single dispersal event. The presence of *Arabis alpina*, however, is the result of at least two colonisations (Koch et al. 2006). Consequently, even the high numbers of colonisation events reported here (13 for *Carex* and four to six for *Ranunculus*) are likely to be underestimates of the real number of colonisations, and therefore of dispersal events, into the high mountain flora of African.

These results illustrate the frequency of multiple recruitments into the African mountains. Nevertheless, single colonisations followed by *in situ* differentiation, which are often associated with the assembly of island floras, have been reported for some plant groups, e.g. *Lychnis* (Popp et al. 2008) and the Giant Senecio, *Dendrosenecio* (Knox and Palmer 1995; Pelser et al. 2007). Many African genera or supra-generic taxa on the high mountains have been established from single colonisations, e.g. the alpine Chironomidae

(Insecta: Diptera) (Eggermont and Verschuren 2007), several flightless insect genera (Brühl 1997), the Ethiopian wolf (*Canis simensis*; Gottelli et al. 2004), and several groups of birds (Fjeldså and Lovett 1997; Johansson et al. 2007; Roy 1997).

Lack of support for dispersal out of the African high mountains

We have little evidence for dispersal out of Africa and out of the African high mountains. Increased taxon sampling and better phylogenetic resolution might yet reveal such events, in particular in *Carex acutiformis* and in the Multifidus- and Oreophytus-clades of *Ranunculus*. The former was thought to occur naturally only in Europe and hence as being introduced to South Africa and North America by European settlers. However, *C. acutiformis* may be nested in a clade with the southern African *C. aethiopica* and *C. drakensbergensis*. Consequently, the most parsimonious interpretation is dispersal from Africa to Europe. Phylogenetic uncertainty also limits our conclusions with regard to the Multifidus- and Oreophytus-clades of *Ranunculus*, and *R. praemorsus* and *R. vaginatus*. The ancestral area reconstructions for some of the most parsimonious trees (though not for the Adams consensus) lead us to infer dispersal out of the African high mountains (for the Adams consensus see Appendix 6, others not shown). Reverse dispersal appears to be similarly rare towards the south, and no instances of dispersal from the African high mountains into the Cape flora have been substantiated (Galley et al. 2007).

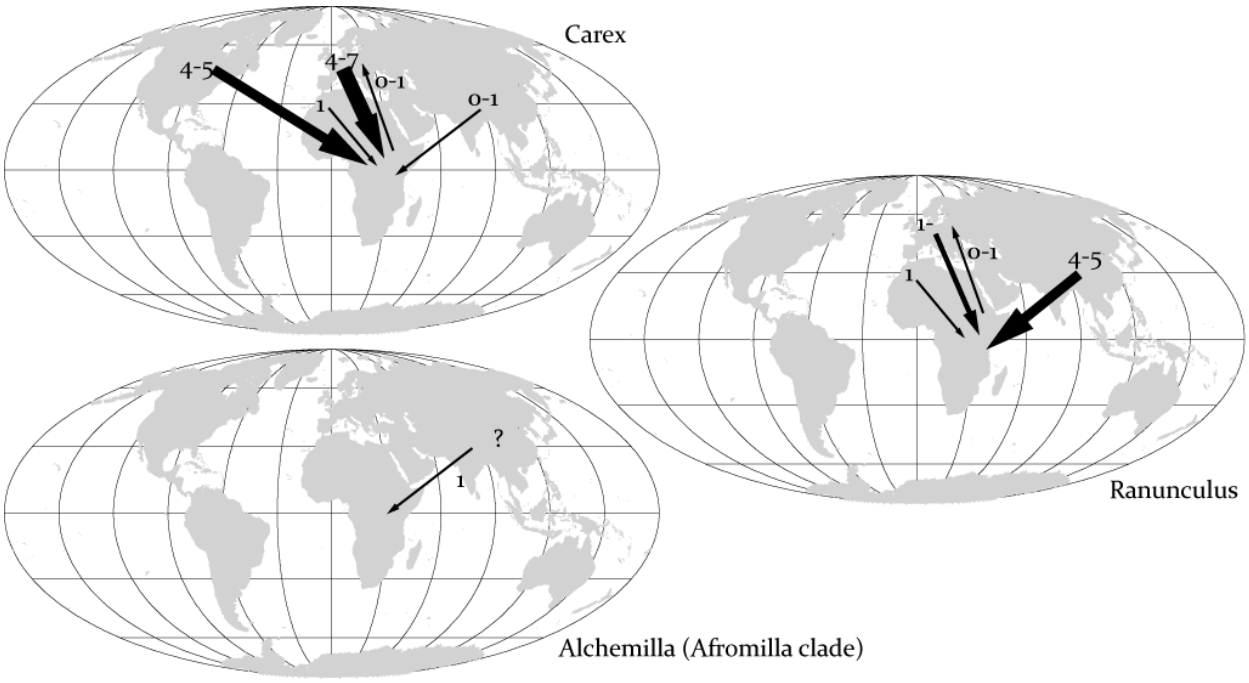

Figure 2: Results of ancestral area reconstructions. Thickness of arrows represents the number of inferred colonisation events into the African high mountain areas.

Contrary to these results, dispersal from islands to the mainland has been reported for both animals (Heaney 2007) and plants (Canary Island: Allan et al. 2004; New Zealand: Winkworth et al. 2002b). There are several possible explanations for this unusual pattern in the African high mountain flora. Firstly, this might be the result of the small total area occupied by the flora of the high mountains in African, and consequently of the low number of species and relatively small populations it supports in relation to other temperate areas. Secondly, the relative youth of the system (which was probably formed during the Plio-Pleistocene) might have reduced the opportunity for dispersal from the high mountains of tropical and southern Africa to other areas.

Table 2: Distance between different putative source regions and the African high mountains

area	**distance**
Western Eurasia	3'500-5'000
Mediterranean	2'000-3'500
Eastern Eurasia	4'000-5'000
temperate North America	11'000-13'000 (Cameroun 10'000)
temperate Hawaii	16'000-18'000
temperate South America	8'000-9'000
Páramo	10'000-12'000
temperate Malenesia	7'000-10'000 (Madagascar 6'000)
aseasonal-wet Australia	10'000-12'000 (Madagascar 9'000)
New Zealand	10'500-13'000

The Holarctic as a source of recruitment of the high mountains in Africa

All clades from the high mountains in Africa in the three pan-temperate genera investigated here were recruited from temperate areas in the Northern Hemisphere. It is interesting that there does not seem to be any recruitment from the mountain areas in the tropics (such as the Andean páramo or Malesian mountain regions) and extra-African southern temperate and mountainous areas (e.g. the Australia or New Zealand Alps, or the southern Andes), even though all three genera are well represented in these areas. The same pattern is shared by other temperate elements in the African sky-islands, such as *Arabis alpina*, *Trifolium, Cardamine* and *Lychnis* (Koch et al. 2006; Ellison et al. 2006; Carlsen 2007; Popp et al. 2008). The predominance of a northern origin for high-montane or alpine floras has also been demonstrated for the Andes (Hughes and Eastwood 2006; Sklenar and Balslev 2007; Von Hagen and Kadereit 2001) and New Zealand (Winkworth et al. 2005). However, clades once established on these mountains often successfully colonise across the southern Pacific Ocean, and across the Tasman Sea (Crisp et al. 2004; Eggens et al. 2007; Glenny 2004; Von Hagen and Kadereit 2001; Winkworth et al. 2005).

This suggests that the cool-climate elements in tropic-alpine and southern temperate regions might be dominated by taxa originating from the Northern Hemisphere. We predict that this also applies to other important alpine-temperate elements such as *Poa, Festuca, Agrostis, Cardamine*, *Cerastium* and *Luzula* (see also Smith and Cleef 1988).

The Northern Hemisphere source areas of *Carex* clades on African high mountains includes not only Eurasia but also North America, which is surprising given the distance between North America and the African mountains (~10'000 km, Table 2). This suggests that either distance alone is not the limiting factor for dispersal in *Carex* or that our ancestral area reconstructions might have been influenced by limited taxon sampling. For example, the high number of inferred colonisation events of *Carex* from North America could be due to the North American bias in taxon sampling, since eastern Eurasian *Carex* is relatively under-sampled. Dispersal from North American to Africa is, however, not without precedent, for example in *Pomaria* (Simpson et al. 2006).

Our results show that the African pan-temperate element as identified by Hedberg (1961) and Engler (1904) are probably entirely Northern Hemisphere derived and therefore Holarctic, making the Holarctic the most important source of lineage recruitment of the African high mountain flora of Tropical and Southern Africa.

CHAPTER 2:

Speciation on African high mountains

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ABSTRACT

Speciation mode and species of diversification have been the centre of attention in many studies, whilst abiotic factors have more often been investigated for their role in species assemblage. We investigate whether, and what, biotic and abiotic factors can be identified which influence speciation on a broader scale. For this we use 12 clades in *Carex* and six in *Ranunculus* that reached the African mountains of sub-Saharan Africa and Madagascar by long distance dispersal. These clades range from lineages that have not diversified to those exhibiting substantial in situ speciation, consisting of up to 12 species. We build generalized linear models to test putative predictors for the variation in these diversifications and their cumulative predictive power. The size of clades in *Carex* and *Ranunculus* on the high mountains of Africa can best be explained by a model combining age and distribution together with water availability and altitude or habitat heterogeneity. This means that most African clades of *Carex* and *Ranunuclus* are simply too young and geographically too restricted to have speciated. Habitat factors seem to influence speciation only in addition to age and distribution.

Keywords: Generalized Linear Model (GLM); *in situ* speciation; monotypic lineages; mountains; polytypic lineages; speciation

INTRODUCTION

The question of what drives speciation is one of the core questions of biology (Darwin 1859). Both mode of speciation, e.g. allopatric speciation, speciation by hybridisation or polyploidisation, etc., and the factors influencing diversification, e.g. the acquisition of key characters, development of a pollination syndrome, etc., have been investigated intensely (Rosenzweig 1995; Ricklefs & Renner 1997; Schluter 2000). Abiotic factors, such as area, elevation, isolation, colonisation/history and age, are more commonly tested for their influence on species richness (Hobohm 2000; Kozak & Wiens 2007; Kreft & Jetz 2007; Ricklefs 2007; Kreft *et al.* 2008) but also have also been used to explain speciation (Juan et al. 2000; Allan et al. 2004; Price & Wagner, 2004; Parent & Crespi, 2006; Heaney, 2007). One of the most debated factors related to diversification is diversity itself (Emerson & Kolm 2005; Emerson & Kolm 2007). The idea of an environmentally determined influence on diversification is less controversial. Habitat heterogeneity has been used as a measure of complexity of these environmental factors because it refers to both the spatial variation and the structural diversity in the environment (Bazzaz, 1975; Schluter, 2000; Kassen et al., 2004; Whittaker et al., 2007). Some authors have even suggested that habitat heterogeneity, rather than area or elevational amplitude *per se*, is the most important predictor of diversification, since habitat heterogeneity usually increases with increasing area and elevation (Tews et al., 2004; Baldi, 2008).

Mountains, like islands, provide a microcosm for the study of evolutionary processes due to their well characterised borders, isolation and structural diversity (Lomolino, 2001; Körner, 2003; Bruun et al., 2006). Many intensively studied islands, such as Hawai'i and the Macaronesian Islands, combine these features; they are not only isolated from a continental flora, they also contain high mountains. The advantage of studying mountains or mountainous islands is their high level of habitat heterogeneity. This is mostly a result of rapid changes in edaphic and climatic factors along altitudinal gradients, associated with high rates of species turnover over short distances. For these reasons, some mountain lineages have comparably high levels of diversity (Hughes & Eastwood, 2006; Moore & Donoghue, 2007; Tkach et al., 2008). One such example is the high mountains of sub-Sahara Africa and Madagascar. These regions consist of a number of 'sky-islands', separated by vast areas of, for montane species, unsuitable dry and warm lowlands. The isolation of the African high mountain areas and ecological differences along altitudinal gradients have been shown to be associated with allopatric speciation and adaptive radiation in the highly specialised Giant Lobelias and Giant Senecios (Knox and Palmer 1995, 1998; Knox 2004).

Studying putative factors for their influence on speciation in groups of closely related species (e.g. sister species or a single radiation) can be informative on a case by case basis, but it fails to address larger-scale patterns (Garland & Adolph 1994).

We therefore explore here differences in clade sizes of 18 African mountain lineages in the two pan-temperate clades, the sedges of the subtribe Cariceae and the buttercups (*Ranunculus*). Gehrke and Linder (submitted) showed that these two clades colonised the African mountains multiple times independently from the temperate areas in the Northern Hemisphere, i.e. at least 12 times in *Carex* and 4-6 times in *Ranunculus*. In both clades, colonisations have led to lineages of various sizes in the high African mountains, ranging from monotypic lineages that have not diversified to clades with up to 12 species. These clades represent multiple independent events with which we can infer general patterns using a statistical approach. We employed a modelling approach using generalized linear models (GLM), with a quasipoisson distribution, to investigate the combined effect of multiple factors on clade size. A number of variables previously associated with diversification were tested as predictive factors (i.e. distribution range, isolation/distance from ancestral area, altitudinal range, number of vegetation zones, number of habitat types, light requirement, water availability and habitat heterogeneity) and their power in predicting clade size was assessed, both alone, and in combination.

METHODS

Taxon sampling

We focused on the pan-temperate genera *Carex* plus *Schoenoxiphium* (Cariceae, Cyperaceae) and *Ranunculus* (Ranunculaceae), because they are species rich, geographically widespread and widely distributed in the African high mountain flora. Molecular phylogenies are available from Gehrke and Linder (submitted) based on nuclear ITS and chloroplast *trn*LF (*Carex*) or *mat*K (*Ranunculus*) sequence data. Phylogenetic relationships were postulated on the basis of parsimony and Bayesian analyses of both plastid and nuclear DNA nucleotide variation. African high mountain clades were identified on the basis of these molecular phylogenetic analyses. The support for clades was assessed by non-parametric bootstrapping methods and Bayesian clade posterior probabilities. All African high mountains clades were additionally tested using parametric bootstrapping.

Carex belongs to the mostly temperate Cyperaceae tribe Cariceae (i.e. the genera *Carex, Cymophyllus, Kobresia, Uncinia* and, the African endemic *Schoenoxiphium*). The Cariceae comprises more than 2000 species (Goetghebeur 1998). About 40 species of *Carex* and 15 species of *Schoenoxiphium* are present on the high mountains in Africa. This excludes the mainly lower montane *Carex* subgenus *Indocarex* (also referred to as section *Vigneastra*). Due to the availability of data from a number of recent molecular phylogenetic studies of Cariceae we were able to include over 600 samples representing ca. 550 species (Gehrke & Linder submitted). Eighty-two of these represent 43 taxa of African high mountains Cariceae, corresponding to 78% of the total number in the region.

Ranunculus (the buttercups), with ca. 600 species, is the largest genus within Ranunculaceae (Tamura 1995). Although buttercups are distributed on all continents, most species occur in temperate to arctic/subantarctic zones (Paun *et al.*, 2005; Hörandl *et al.* 2005). They are found in various terrestrial or aquatic habitats, from lowlands to high alpine zones, as well as on high mountains in the tropics. The 230 *Ranunculus* species included in the analyses represent material from all continents including representatives of all subgenera and sections. Sixteen of the 20 high mountain taxa in Africa were included (~80%).

The sampling of African high mountain species in the molecular phylogenetic analyses was high (~75%) (Gehrke and Linder, submitted). Nevertheless, all analyses were performed using both the clade size as represented in the phylogenies (observed clade size), plus estimated clade sizes (Table 1) in order to correct for incomplete taxon sampling. Estimations of clade size are based on sectional classifications of the species which were not sampled, as obtained from the taxonomic literature (Kükenthal, 1909; Hedberg, 1957), and on morphological characteristics. We used both a conservative and a high estimate of species numbers in order to avoid possible Type I or Type II errors resulting from limitation in the taxonomic knowledge of the African mountain flora. Taxa which could not be placed with some confidence were not included in the analyses, for example *C. johnstonii,* the phylogenetic position of which is uncertain and *C. zuluensis,* which might be a member of the *Schoenoxiphium* clade. It is unclear whether *R. oreophytus* and *R. rarae* should be considered one or two clades as their sister-relationship is not supported. Consequently, we duplicated all analyses with these two species treated both as separate monotypic lineages, and as a clade of two species. These two treatments are represented in all tables 1) as *R. rarae* and 2) as *R. rarae* plus *R. oreophytus* as the Oreophytus clade (Table 1, 2 and 3).

Divergence time estimates

We used the molecular datasets to estimate the relative ages of the African clades. Multiple accessions were deleted in order to avoid their influence on the relative dating (Linder et al., 2005). We used two different approaches to obtain estimates of branch lengths from which to estimate the relative ages of the nodes. In the first approach, we estimated the best fitting model of sequence evolution given the data and the topology of an arbitrarily chosen most parsimonious tree using MODELTEST (Posada & Crandall, 1998). Branch lengths were then calculated under the likelihood optimality criterion in PAUP* (Swofford, 2001), using a) the original data and b) 100 bootstrap re-sampled data matrices (in order to obtain confidence intervals for the estimate). The second approach was based on the tree from the Bayesian analysis with the best log likelihood score and 100 randomly selected trees from the post-burn-in sample to be used for the calculation of confidence intervals.

In both cases the molecular clock was rejected using a likelihood ratio test, and we therefore rate corrected the trees using Penalized Likelihood (PL) (Sanderson, 2002) as implemented in r8s (Sanderson, 2003).

Cross validation was used to determine the appropriate smoothing parameter value. The root node was fixed to one to obtain relative (rather than absolute) ages. Confidence intervals were calculated for selected nodes by summarising the estimates based on the a) 100 bootstrap re-sampled trees and b) 100 Bayesian trees, using the 'profile' command in r8s.

Table 1 African clades of *Carex* and *Ranunculus* and species representing these in the molecular phylogenetic analyses of Gehrke and Linder (Chapter 1). Bootstrap support values and Baysian clade credabilities of the monophyly of the clades in the combined analyses of ITS and trnLF are given. Bootstrap support values are indicated at the left and Bayesian clade credabilities in brackets. Clades with higher support for one marker region are marked with an asterisk and the value given after the slash. Abbreviations for the parsimony ancestral area reconstructed are: E Eura.=eastern Eurasia, W. Eura.=western Eurasia, Med.=Mediterranean and Northern Africa, N-Am.= North America.

clade names	Taxa in analysis	support	ancestral area
Carex			
Acutiformis-clade	*C. acutiformis, C. aethiopica* & C. *drakensbergensis*	66/89*(--)	N-Am./E.Eura.
Bequaertii-clade	*C. bequaertii*	99 (1.00)	W.Eura.
Cognata-clade	*C. cognata, C. phragmitoides, C. sphaerogyna* & *C. subinflata*	70 (--)	N-Am.
Conferta-clade	*C. conferta*, *C. leptosaccus* and *C. lycurus*	81/91*(0.99)	N-Am.
Erythrorrhiza-clade	*C. erythrorrhiza*	100 (--)	W.Eura./Med.
Glomerabilis-clade	*C. glomerabilis*	97 (1.00)	W.Eura/Med.
Johnstonii-clade	*C. johnstonii*	99 (1.00)	W.Eura
Madagascariensis-clade	*C. austro-africana, C. baronii* & *C. madagascariensis*	58 (--)	N-Am.
Monotropa-clade	*C. monotropa*	1 accession	W.Eura.
Monostachya-clade	*C. monostachya* & *C. runssoroensis*	100 (1.00)	N-Am.
Peregrina-clade	*C. peregrina*	100 (1.00)	W.Eura.
Simensis-clade	*C. petitiana, C. longipedunculata, C. mannii, C. ninagongensis, C. simensis*, *C. sp.*& *C. vallis-rosetto*	--/67* (0.93)	Med.
Schoenoxiphium	18 species of the genus *Schoenoxiphium*	-- (0.99)	W.Eura.
Ranunculus			
Meyeri-clade	*R. meyeri*	1 accession	E.Eura.
Multifidus-clade	*R. aberdaricus, R. bequaertii R. pinnatus,* & *R. multifidus*	97/0.98	E.Eura.
Oreophytus-clade	*R. oreophytus* & *R. rarae*	-- (--)	E.Eura. (0-2)
Rarae-clade	*R. rarae*	67/1.00	Med.
Stagnalis-clade	*R. cuneilobus, R. cryptanthus, R. simensis, R. stagnalis* & *R. tembensis*	1 accession	W.Eura.
Trichophyllus-clade	*R. tichophyllus*	1 accession	W.Eura.
Volkensii-clade	*R. volkensii*	86 (1.00)	E.Eura.

All dates reported for correlation analysis are stem ages, representing the maximum time elapsed since colonisation of the high mountains in Africa. The degree to which these stem age estimations will overestimate the true timing of colonisation cannot be known, as it depends on the degree to which colonisation is predated by the age of the non-African sister-groups and on the amount of extinction. Although the crown ages can be determined with more accuracy, these are not appropriate here, as monotypic lineages do not have crown ages.

Scoring of variables

Data on abiotic and biotic factors were scored from taxonomic revisions and floras (Chermezon, 1937; Milne-Redhead and Turrill 1952; Hedberg, 1957; 1966-; Haines & Lye, 1983; Lye 1997; Cable & Cheek, 1998; Cheek, 2000; African Flowering Plant Database, 2008; chapter 4). In addition, we included information from herbarium specimen labels and own field observations during field work in Africa 2004-2007. We scored eight different variables. Seven are simple standardized measures; these are distribution range, isolation/distance from ancestral area, altitudinal range, number of vegetation zones, number of habitat types, light requirement, water availability. The last, habitat heterogeneity, is the sum of the last five measures (for details see Appendix 7).

Statistical approach

We used generalized linear models (GLM) in R version 2.6.2 (R Development Core Team 2008) to build models including the different variable(s) that might predict clade size. We first assumed a poisson distribution of the data and analysed the distribution of residuals to confirm the distribution. As some combinations show overdispersion, a quasipoisson distribution with loglink was used. Transformation of the data using the natural log, arcsine and square root were inspected but rejected, as untransformed data conformed best to the assumed distribution. All variables were tested alone and in combination. As the Akaike Information Criterion (AIC) cannot be calculated under a quasipoisson distribution, the deviance (D^2) was calculated and used for model comparisons between models of the same complexity. The adjusted D^2 (based on S-Plus Function for calculating an adjusted D^2 see Hastie & Pregibon 1998) was used when comparing models of different levels of complexity to avoid interpreting an increase of the D^2 as an increase of model fit in cases where it represents over-fitting of the model. Kendall's rank correlation tau were used to assess correlation between different predictors of clade size.

Table 2: Scoring of the different variables for *Carex* and *Ranunculus* clades. *Carex* lineages are indicated by (*C.*), lineages in Ranunculus by (*R.*). The response variable clades size is represented: clade size in analyses – conservative estimated clade size (high estimated clade size). Standard-deviation of the relative age estimations are given in brackets.

	Clade size analy. - cons. (high)	Relative age (std.)		Distri-bution range	Isolation	Altitudinal range (m)	No. of altitudinal zones	No. of habitat types	Light require-ment	Water availa-bility	Habitat hetero-geneity
		Parsimony	*Bayesian*								
C. bequaertii (*C.*)	1-2 (3)	0,28 (0,07)	0,31 (0,01)	3	4‘000	2‘000	4	2	3	2	11
C. erytrorrhiza (*C.*)	1-1(1)	0,28 (0,06)	0,33 (0,01)	1	3‘500	1‘000	3	2	1	2	8
C. glomerabilis (*C.*)	1-1 (2)	0,29 (0,09)	0,35 (0,04)	1	3‘500	2‘000	2	1	2	3	8
C. johnstonii (*C.*)	1-1(2)	0,70 (0,05)	0,75 (0,02)	4	4‘000	1‘000	2	2	3	2	9
C. monotropa (*C.*)	1-1(1)	0,16 (0,10)	0,29 (0,06)	1	4‘000	1‘000	2	1	1	2	6
C. peregrina (*C.*)	1-1(1)	0,26 (0,05)	0,19 (0,01)	2	4‘000	2‘000	2	2	4	2	10
Acutiformis-clade (*C.*)	3-4 (5)	0,38 (0,01)	0,41 (0,03)	1	4‘500	3‘000	2	3	2	2	9
Cognata-clade (*C.*)	4-5 (6)	0,29 (0,06)	0,63 (0,02)	7	12‘000	2‘000	2	2	1	2	7
Conferta-clade (*C.*)	3-3 (4)	0,48 (0,04)	0,40 (0,02)	4	12‘000	2‘000	5	2	2	2	11
Madagascari.-clade (*C.*)	3-4 (5)	0,77 (0,03)	0,63 (0,02)	3	12‘000	2‘000	2	4	3	3	12
Monostachya-clade (*C.*)	2-2 (3)	0,25 (0,04)	0,04 (0,00)	3	12‘000	1‘500	2	1	1	3	7
Schoenoxiphium (*C.*)	18-25 (35)	0,83 (0,04)	0,82 (0,02)	7	4‘000	2‘000	2	3	3	3	11
Simensis-clade (*C.*)	8-8 (12)	0,23 (0,06)	0,54 (0,03)	6	3‘000	3‘000	5	3	3	3	14
R. meyeri (*R.*)	1-1(1)	0,52 (0,05)	0,22 (0,03)	1	4‘500	1‘000	2	1	1	2	6
R. rarae (*R.*)	1-1(1)	0,56 (0,04)	0,20 (0,02)	1	3‘000	500	2	1	1	2	6
R. trichophyllus (*R.*)	1-1(1)	0,18 (0,05)	0,10 (0,01)	1	4‘000	500	1	1	1	1	4
R. volkensii (*R.*)	1-1 (2)	0,48 (0,06)	0,20 (0,03)	3	4‘500	2‘000	2	2	2	2	8
Multifidus-clade (*R.*)	4-6 (8)	0,58 (0,03)	0,17 (0,01)	8	4‘500	3‘000	2	3	4	3	12
Oreophytus-clade (*R.*)	2-2 (3)	0,58 (0,04)	0,16 (0,01)	4	4‘500	2‘500	4	2	1	1	8
Stagnalis-clade	5-7 (8)	0,35 (0,05)	0,10 (0,01)	3	4‘000	2‘000	4	3	2	2	11

RESULTS

Speciation in African high mountain lineages

In total, about half of the taxa in *Carex* and *Ranunculus* that have colonised the high mountains in Africa have led to lineages with a single species whereas the other half of the colonisation events have led to more extensive *in situ* speciation. In *Carex*, *in situ* speciation events have contributed more than 85% of the observed species richness in the African sky-islands. In *Ranunculus* lineages with more than one species account for 60-70% of all taxa in the high mountain region of Africa.

Relative dating

Different age estimates did not result in significant differences in the GLMs. Therefore we report here only on the ages determined using the first method (i.e., based on the parsimony topology; Table 2). Full details of all results using both methods can be found in Appendix 8. As we have only relative and not absolute ages, direct comparison between *Carex* and *Ranunculus* is not possible.

Distribution

All high mountain regions of Africa have clades with more than one species. Monotypic lineages in Africa are absent from West Africa, the Chimanimani region of Zimbabwe, and Madagascar. The highest number of lineages without *in situ* diversification in the high African mountains occur in Ethiopia (i.e. six lineages, three of which are endemic) followed by Imatong-Usambara (five lineages, one endemic), Southern Africa (three endemic lineages), Uluguru-Mlanje (three lineages, one endemic) and Kivu-Ruwenzori (three lineages, none endemic). Higher mountain regions (i.e. Central East Africa, Ethiopia and South Africa) contain more lineages than lower areas (i.e. Madagascar, Southern East Africa and Chimanimani area), with the exception of Mt. Cameroon in West Africa which is over 4000m in altitude but lacks monotypic lineages. The absence of many lineages from West Africa could be due to young age and recent disturbance, as it still has ongoing volcanic activity which might have led to high extinction. The overall number of lineages in the area is also low.

GLM regressions

Among the significant models for *Carex* and *Ranunculus*, the best was selected to maximize both the D2 and adjusted D2. These include age, distribution range and water availability plus altitudinal range or habitat heterogeneity (see Table 3 and Appendix 7).

In *Carex* the model "age, distribution range, water availability and altitudinal range" was slightly better than the more complex model (i.e., also including habitat heterogeneity) for all clade size estimations. In *Ranunculus* "age, distribution range and water availability" was the best model with a significant intercept for conservative estimated clade size and clade size in analyses, while for the high estimated clade size habitat heterogeneity was additionally included in the best model. Residual deviance statistics of the best model can be found in Figure 1.

The influence of each data point on the analyses was assessed by the sequential deletion and replacement of the relevant data points. The only effect of excluding clades was some variation in the D^2. The greatest influence was exerted by the exclusion of the *Carex* Simensis-clade and not the exclusion of *Schoenoxiphium* as might be expected from visual inspection of the data.

Kendall's rank correlation showed no significant p-value ($p<0.05$) for age with any other predictor variable (Appendix 8) in *Carex* and in *Ranunculus* and no significant correlation between distribution range, isolation, altitudinal range and water availability with any other predictor variable in *Carex*. There is a positive correlation between habitat heterogeneity, number of habitats and light requirement, as well as altitudinal zones with the number of habitats and with habitat heterogeneity.

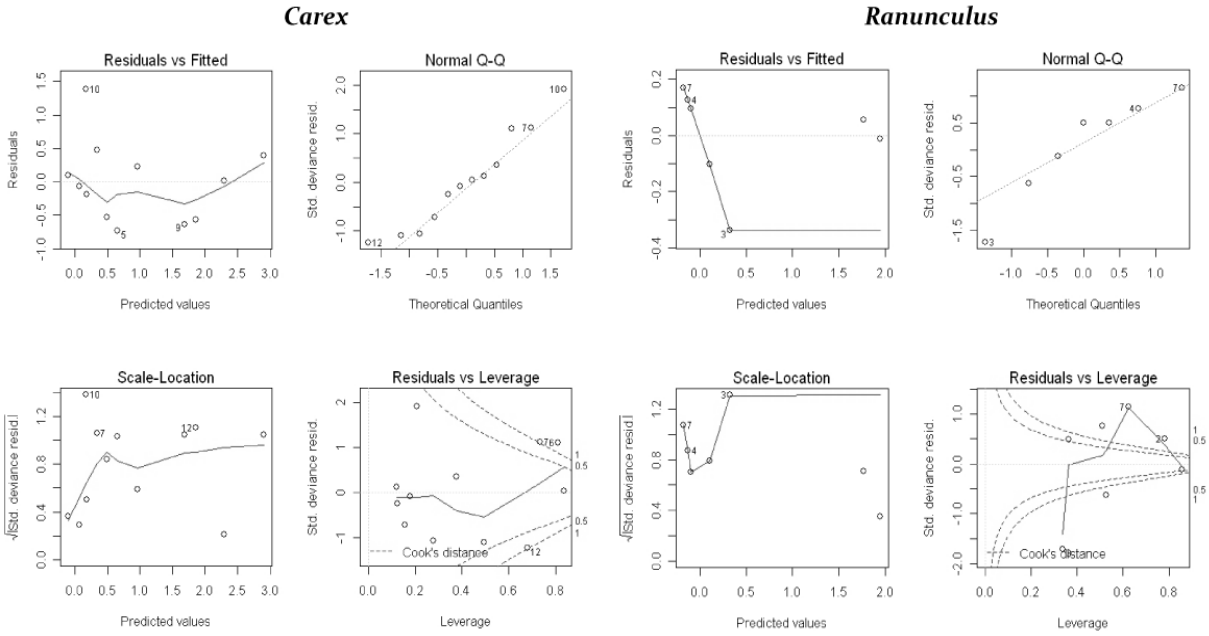

Figure 1: Results of residual deviance inspection of the best model in the generalized linear model (GLM) for *Carex* and *Ranunculus*.

In *Ranunculus* distribution range shows a significant positive correlation of distribution range with altitudinal zone, water availability and habitat heterogeneity. Altitudinal zone, altitudinal range and water availability are correlated, as well as habitat heterogeneity with altitudinal zones and with water availability.

Table 3: Generalized linear models (GLM) using quasipoisson distribution with loglink. Disp.=dispersion parameter for quasipoisson family; sig.=coefficient significance of the intercept; RD= residual deviance; D^2=devianz; aD^2=adjusted D^2; distr.=distribution range; zones=number of altitudinal zones; range=altitudinal range; types=number of habitat types occupied; light=light requirement; water=water availability; hab.=habitat heterogeneity. Intercept significance value > 0.05 are marked in bold and with an asteriks. See supplement 2 for full details.

	Carex					***Ranunculus***				
	disp.	sig.	RD	D^2	aD^2	*disp.*	*sig.*	*RD*	*D^2*	*aD^2*
estimated clade size										
age+distr.+water+zones + range	0.420	**0.005***	2.312	0.959	0.925	*0.147*	*0.317*	*0.154*	*0.990*	*0.937*
age+distr.+water+zones + hab.	0.893	**0.045***	4.154	0.926	0.865	*0.051*	*0.217*	*0.052*	*0.996*	*0.979*
age+distr.+water+range	**0.367**	**0.003***	**2.354**	**0.958**	**0.935**	*0.088*	*0.137*	*0.184*	*0.988*	*0.963*
age+distr.+water+zones	0.916	**0.038***	4.590	0.919	0.872	*0.085*	*0.147*	*0.177*	*0.988*	*0.964*
age+distr.+water+hab.	0.788	**0.026***	4.180	0.926	0.884	*0.082*	*0.190*	*0.169*	*0.989*	*0.967*
age+distr.+water	0.850	**0.036***	5.146	0.909	0.875	***0.059***	***0.029****	***0.184***	***0.988***	***0.975***
age+distr.+range	0.436	**0.004***	3.150	0.944	0.923	*0.418*	*0.522*	*1.267*	*0.914*	*0.828*
age+distr.+hab.	0.723	**0.022***	7.210	0.912	0.825	*0.473*	*0.588*	*1.440*	*0.902*	*0.805*
distr.+zones+types	0.750	**0.022***	5.752	0.898	0.860	*0.160*	*0.021**	*0.503*	*0.932*	*0.966*
clade size in analysis										
age+distr.+water+zones + range	0.528	**0.016***	3.036	0.936	0.882	*0.081*	*0.299*	*0.084*	*0.989*	*0.935*
age+distr.+water+range	**0.458**	**0.009***	**3.057**	**0.935**	**0.899**	*0.050*	*0.126*	*0.104*	*0.987*	*0.960*
age+distr.+water+hab.	0.845	**0.049***	4.641	0.902	0.846	*0.284*	*0.558*	*0.886*	*0.886*	*0.772*
age+distr.+water	0.722	**0.026***	5.098	0.892	0.852	***0.037***	***0.044****	***0.115***	***0.985***	***0.971***
high estimated cladesize										
age+distr.+water+zones + range	0.497	**0.005***	2.966	0.965	0.936	*0.043*	*0.187*	*0.044*	*0.997*	*0.985*
age+distr.+water+zones	1.322	0.059	6.563	0.923	0.879	*0.025*	***0.050****	*0.050*	*0.997*	*0.991*
age+distr.+water+range	**0.435**	**0.002***	**3.002**	**0.965**	**0.944**	*0.024*	***0.039****	*0.049*	*0.997*	*0.992*
age+distr.+water+hab.	1.186	**0.048***	6.407	0.925	0.881	***0.019***	***0.048****	***0.038***	***0.998***	***0.993***
age+distr.+water	1.217	0.061	7.483	0.912	0.879	*0.059*	***0.029****	*0.184*	*0.988*	*0.975*

DISCUSSION

The influence of time on plant lineages in the African mountains

The models reported above suggest an overall importance of time in the *in situ* diversification of pan-temperate floral elements in the African high mountain regions. This is consistent with the observation that age is an important factor in influencing clade sizes (Willis 1922). It has further been hypothesised that over longer time-spans speciation is a more dominant mechanism than colonisation in generating diversity on islands (Macarthur & Wilson 1967; Emerson & Oromi 2005). This is also consistent with the patterns in the major animal clades, where diversity is the result of clade longevity, rather than differences in speciation rate (McPeek 2007).

However, the impact of age might not only be due to clade longevity but might also be due to historical processes, i.e. immigration history or niche pre-emption (Silvertown, 2004; Silvertown et al., 2005; Fukami et al. 2007).

Estimating the amount of in situ speciation in a clade is beset with problems, in particular due to the effects of extinction and of multiple colonisations within a taxon. Some single endemic species may merely be the surviving members of once larger clades reduced though extinction. Conversely, phylogenetic studies have demonstrated that it is not safe to assume that groups with more than one species on an island have been derived from a single colonisation event (Emerson, 2002; Heaney, 2007; Alsos et al., 2007). Even when island lineages are demonstrably monophyletic, this might be due to persistence of species rather than in situ speciation (Emerson, 2005). Furthermore, the species of an African mountain clade could have been derived from multiple independent colonisations of the African sky-islands if extinction in the source area has been relatively high. This might be a plausible scenario for the groups studied here, given that glacial cycles may have led to a high degree of extinction in the Northern Hemisphere. However, the relevant fossil record is too fragmentary to be able to test this for the groups analysed here, and we have little choice but to interpret our results at face value.

The influence of distribution range

Carex and *Ranunculus* show a positive response of clade size to distribution range (Appendix 7). Distribution range is also part of the best model in both groups. One interpretation is that distribution here reflects allopatric speciation; a second could be that available area *per se* has a positive influence on speciation; third that habitat heterogeneity increases with area such that the effect of habitat heterogeneity is measured rather than the effect of area itself (Baldi, 2008). It is unlikely that distribution range is simply correlated to clade size because larger clades (i.e. more species) have a higher chance for dispersal than smaller clades (i.e. fewer species). If this would be the case then we would

not expect a significant higher D^2 and adjusted D^2 than in the simpler models without distribution range.

Since we are scoring mountain ranges for whole lineages instead of using total land area of individual species we are able to show overall patterns of speciation. However, this approach does not allow us to discern between the effect of area itself, dispersal ability or disjunct distribution which might have led to allopatric speciation. For this we would have to compare the range of sister species (Felsenstein 1985) which is not possible due to limitations of phylogenetic resolution at this level. We therefore investigated the distribution of individual species in the different lineages. Most species within an African mountain clade have overlapping distributions, but 30% of all lineages included in the analyses are restricted to a single mountain system (however only one out of the 19 lineages is restricted to single mountain range). Thus, on the basis of the currently available data, allopatric speciation is neither supported nor rejected and backward dispersal after speciation cannot be ruled out. In contrat, the combination of allopatric speciation after range expansion to different mountains followed by adaptive radiation has been shown to be the predominant form of speciation in African mountains for Giant Lobelias and Giant Senecios (Knox 2004), as well as for other island systems such as Hawai'i (Price and Wagner 2004) or the Canary Islands (Juan et al. 2000). However, species of *Carex* and *Ranunuclus* have much less restricted distribution ranges than most of the species included in those studies.

We can further show that habitat heterogeneity is not the cause of the area effect observed here: replacing distribution by habitat heterogeneity does not lead to a similar D^2 and adjusted D^2, and there is no co-variation between the two factors ($p<0.05$). Our interpretation of these results is that once a lineage has become established in the high mountains of Africa, its dispersal ability has an important influence on its ability to speciate further. Reaching other distant mountain regions in Africa can lead to establishing new populations which over time can lead to speciation (allopatry) or reaching new mountain ranges might lead to reaching habitats with unoccupied niches.

Is habitat heterogeneity driving diversification in the African sky-islands?

Habitat heterogeneity is not part of the overall best model in either *Carex* or *Ranunculus*, with the exception of the high estimated clade size in the *Ranunculus,* in which habitat heterogeneity is part of the overall best model together with age, distribution range and water availability (Table 3). Habitat heterogeneity might nevertheless still have some influence since it is a compound factor, one component of which (water availability) does figure in the best model. Water availability is often influenced by other factors, such as altitude and exposition, of which the latter was not scored separately in these analyses.

The number of altitudinal zones and altitudinal range as measures of elevation do not seem to have a strong influence on speciation in *Carex* and *Ranunculus* in the African high mountains. The numbers of altitudinal zones and/or the altitudinal range are part of the best model in *Carex* but not in *Ranunculus*. This result contrasts with those of previous studies showing a positive correlation with species richness of islands (Kalmar & Currie, 2006; Kreft et al., 2008) and an influence on diversification (Von Hagen & Kadereit 2001; Hughes & Eastwood, 2006).

The Kendall's rank correlation showed a significant p-value ($p<0.05$) for habitat heterogeneity and altitudinal range in *Carex* and habitat heterogeneity and altitudinal zones in *Ranunculus* (Appendix 8). This is also reflected in the view that the impact of elevation can be ascribed to the increase in habitat heterogeneity (Stuessy et al. 2006). This follows the same argument as for area, i.e., higher islands generally have greater habitat diversity, and this stimulates speciation (e.g. in Hawaii). Lower islands with more uniform environments, by contrast, contain fewer species and more lineages without *in situ* diversification (e.g. in Ullung Island), i.e. low habitat diversity restricts speciation.

The positive influence of habitat heterogeneity or one of its constituent factors (such as water availability or altitudinal zones) might be an indication of adaptive radiation. It is however not possible to establish a direct link between habitat heterogeneity and adaptation to specific habitats, for the same reasons as for the example of distribution and allopatric speciation described above. The GLM modelling allows us to infer broad patterns based on repeated events, but it does not tell us about the mode of speciation. Most species within lineages of *Carex* and *Ranunuclus* have overlapping habitats as well as distribution ranges and ecological speciation can neither be ruled out nor supported. This is different to the situation of the Giant Lobelias and Giant Senecios investigated by Knox (2004), where clear separation in distribution range and habitat have led to the hypothesis that allopatric speciation and adaptive radiation have shaped the flora of the Eastern African mountains.

Conclusion: What is driving speciation on the African high mountains

Overall, the diversification of the pan-temperate floral elements on the high mountains of Africa is influenced by a combination of clade age, distribution/dispersal ability, and habitat heterogeneity (i.e. water availability and altitudinal zone). Our approach shows the importance of model building for addressing long standing questions in evolution, such as inferring factors which influence speciation. Only under such an approach can it be determined if some factors show their main effect after taking other more prominent influences into account.

CHAPTER 3:

Molecular phylogenetics of *Alchemilla*, *Aphanes* and *Lachemilla* (Rosaceae) inferred from plastid and nuclear intron and spacer DNA sequences, with comments on generic classification

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Mol. Phylogenet. Evol. 47:1030-1044.

ABSTRACT

Alchemilla (the lady's mantles) is a well known but inconspicuous group in the Rosaceae, notable for its ornamental leaves and pharmaceutical properties. The systematics of *Alchemilla* has remained poorly understood, most likely due to confusion resulting from apomixis, polyploidisation, and hybridisation, which are frequently observed in the group, and which have led to the description of a large number of (micro-) species. A molecular phylogeny of the genus, including all sections of *Alchemilla* and *Lachemilla* as well as five representatives of *Aphanes*, based on the analysis of the chloroplast trnL-trnF and the nuclear ITS regions is presented here. Gene phylogenies reconstructed from the nuclear and chloroplast sequence data were largely congruent. Limited conflict between the data partitions was observed with respect to a small number of taxa. This is likely to be the result of hybridisation/introgression or incomplete lineage sorting. Four distinct clades were resolved, corresponding to major geographical division and life forms: Eurasian *Alchemilla*, annual *Aphanes*, South American *Lachemilla* and African *Alchemilla*. We argue for a wider circumscription of the genus *Alchemilla*, including *Lachemilla* and *Aphanes*, based on the morphology and the phylogenetic relationships between the different clades.

Keywords: *Alchemilla*; *Lachemilla*; *Aphanes*; Alchemillinae; Rosaceae; molecular phylogeny; generic delimitation; apomixes

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INTRODUCTION

The genus *Alchemilla* in the wide sense (Rosaceae), by some authors recognised as the subtribe *Alchemillinae* including *Alchemilla*, *Lachemilla* and *Aphanes* (e.g. Notov and Kusnetzova 2004), is notable for its highly derived but inconspicuous flowers. *Alchemilla* was previously thought to be related to the Sanguisorbinae (e.g. Hutchinson 1964) due to superficial similarity caused by reduction in flower parts. However, its relation to Potentilleae was noted by Schulz-Menz (1964) and the position later confirmed by DNA sequence data (Eriksson et al. 1998; 2003). The petals of *Alchemilla, Lachemilla* and *Aphanes* are lacking and the two whorls of four calyx and four epicalyx lobes form a hypanthium. One to four or more introrse or extrorse stamens are inserted at the inner or outer side of a flower disc and one to many carpels are present (Figure 1). *Alchemilla* is a well known example of polyploidy and it is probably the best known group with autonomous apomixis (in the sense of agamospermy, in which endosperm formation is independent of the fertilization of the primary endosperm nuclei) in the Rosaceae (Czapik 1996). In most plants apomixis is not strictly obligate but facultative to a varying extent (Asker and Jerling 1992; Mogie 1992; Richards 2003, Hörandl 2004 and many others), although this might not apply to autonomous apomicts in cases where no viable pollen is produced, as for most Eurasian *Alchemilla* species but could be the case for *Aphane*s or *Lachemilla*. In addition to (in-) complete apomixis and poly- or aneuploidy, many species of *Alchemilla* can grow clonally, they display heteroblastic plasticity (such as differing morphologies of leaves), and show variability of indumentum and instability in flower characters. The difficulties inherent in interpreting this kind of variation have led to the description of many microspecies and species complexes, a problem often associated with agamic species complexes (Asker and Jerling 1992; Hörandl 2004).

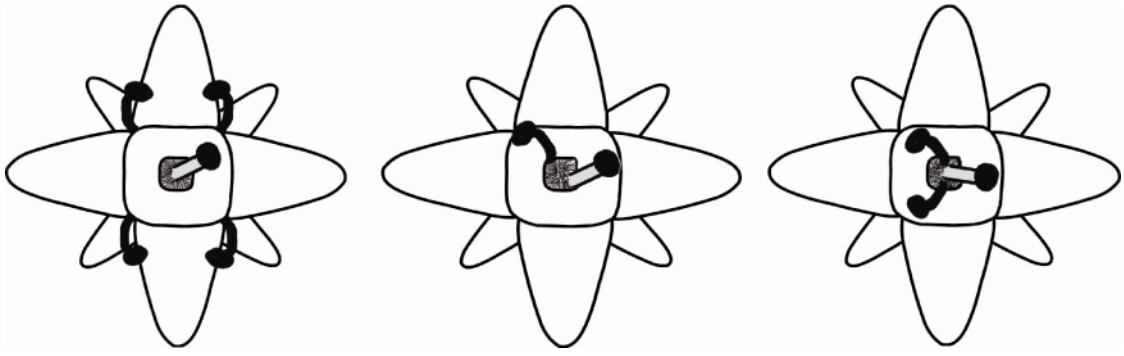

Figure 1: Schematic drawing of *Alchemilla* flowers. From left to right Eurasian and African *Alchemilla* A4 G1 (-4-12) stamens introse; *Aphanes* A1 G1 stamens extrose; *Lachemilla* A2 (3-4) G1-2 (-8) stamens extrose

***Alchemilla* L.**

The genus *Alchemilla* was described by Linnaeus (1753) and currently includes at least 250 (-1000) species (Fröhner 1995a). Some earlier authors referred to this group as *Eualchemilla* (Table 1). It has a mainly Holarctic distribution with a centre of species richness in western Eurasia but occurs also in South India, Sri Lanka, Java, China and Japan and on the mountains of Africa and Madagascar (Figure 2). *Alchemilla* is characterised by introrse stamens that are inserted at the outer side of the discus (Figure 1). However, specimens have been reported which also possess stamens at the inner side of the discus (Fröhner 1995a). Stamens that are inserted at the outer side of the discus is common in *Potentilla* and probably represents the pleisiomorphic character state. A monograph or revision has yet to be accomplished for the whole genus, but various less than comprehensive treatments have been produced by different authors (Table 1). Linnaeus (1753) mentioned three representatives *A. vulgaris*, *A. alpina* and *A. pentaphyllea* (Figure 3). Many of the earliest authors have followed this division into three groups of species in the Eurasian *Alchemilla* on the basis of the level of dissection of their leaves (Focke 1888; Buser 1892; Rothmaler 1934).

Table 1: Classification of *Alchemilla* in the wide sense used by different authors

Author	***Alchemilla***	***Aphanes***	Lachemilla	***others***
Linnaeus 1753	Genus	Genus	-	-
Scopoli 1772	Genus	-	-	-
Persoon 1805	Genus	*Genus*	*in* Aphanes	-
De Candolle 1825	Section	Section	in *Alchemilla*	-
Focke 1888	Section *Eualchemilla*	Section	Section	-
Lagerheim 1894	Subgenus *Alchemilla,* Section *Eualchemilla*	Subgenus *Alchemilla,* Sect. *Aphanes*	Subgenus *Lachemilla,* Section *Fockella,* Section *Eulachemilla*	-
Rydberg 1908	Genus	Genus	Genus	Zygalchemilla
Murbeck 1915	Section	*Section*	*in* Aphanes	Section *Fockella*
Perry 1929	Section	Section	Section (6 Series.)	
Rothmaler 1935	Subgenus (6 Sect.)	Subgenus (3 Sect.)	Subgenus (5 Sect.)	-
Haumann et Balle 1936	Subgenus *Eualchemilla*	Subgenus	?	-
Rothmaler 1937	Genus	Genus	Genus (6 Sect.)	-
Fröhner 1995	Genus (18 Sect.)	Genus (3 Sect.)	Genus (6 Sect.)	-
Kalkman 2004	Subgenus	Subgenus.	Subgenus	-
Notov 2004	Genus (7 Sect.)	Genus (3 Sect.)	Genus (6 Sect.)	-

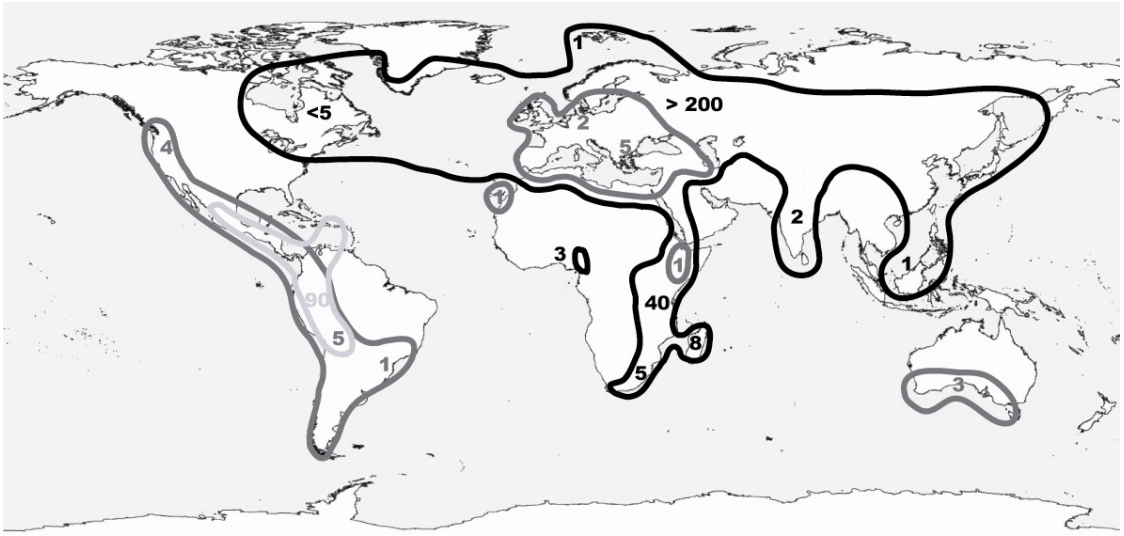

Figure 2: Distribution of *Alchemilla*. Black lines Eurasian and African *Alchemilla*, grey lines *Aphanes* and light grey *Lachemilla*. Numbers indicate number of species in the area.

All authors agree in placing the species from tropical and southern Africa in sections separate to those of the Eurasian species (Table 2), based on their distributions and the occurence of longer internodes in many species. However, no consistent diagnostic characters have been proposed for the African sections combined, nor has it been suggested that all African sections should be recognised together as separate taxa in their own right (Fröhner 1986). Nevertheless, the African species display greater morphological variation than those found in Eurasia. They include many dwarf shrubs and trailing herbs that are often dominant species in the Afrotemperate Regions.

***Aphanes* L.**

Aphanes is a small group of about 20 species distributed in temperate regions across the world. The centre of species diversity is found in the western Mediterranean (Europe and North Africa). Two species occur throughout northern and central Europe, four on the pacific coast of North America, five in western South America, one in eastern South America (south Brazil to southern Argentina) and three in southern Australia (Figure 2). Three sections are recognised according to Fröhner (1986): *Aphanes*, *Quadridentatae* and *Aequidentatae*.

The plants are mostly very small, sometimes no more than a few centimetres in height and annual or biennial (Peter Frost-Olsen pers. comm.). The flowers are similar to those of *Alchemilla*, but they have only a single extrorse episepal stamen at the inner part of the discus, and a single stigma is formed by the only carpel (Figure 1).

Figure 3: Pictures of the *Alchemilla* in the wide sense: A *A. pentaphyllea*; B *A. alpina*; C *A. hybrida*; D *L. orbiculata*; E *L. polylepis*; F *Ap. arvensis*; G *A. argyrophylla.* Pictures A, B, C, F and G from B. Gehrke; D from K. Romoleroux and L from A. Groeger.

Occasional reports of multiple carpels in *Aphanes* have by some authors been thought to stem from the inclusion of *Lachemilla* (Fröhner 1995), even though it is not uncommon to find plants where all flowers have 2 carpels, especially in *Ap. arvensis* (Peter Frost-Olsen pers. comm.). In *Aphanes,* as opposed to *Alchemilla*, pseudogamous apomixis has been reported, in which pollination is necessary for endosperm formation, as the polar nuclei must be fertilised to ensure formation of viable seeds (Asker and Jerling 1992). Unlike in *Alchemilla* diploid species with 2n=16 exist in *Aphanes* in addition to tetraploids and hexaploids.

Lachemilla Focke

Lachemilla is a group of ca. 80 morphologically variable perennial herbs and shrubs. They are distributed in South and Central America from Mexico and the Greater Antilles (Hispaniola) to the Andes of northern Chile and Argentina, between 2200 and 5000 m in elevation, where they can form dense stands. *Lachemilla* is considered one of the most important and most species rich groups of plants in the andean páramos (Albach and Chase 2004; Romoleroux 2004).

Lachemilla has sometimes been included in *Alchemilla* (Linnaeus 1753; Focke 1888; Fedde 1910; Perry 1929) or *Aphanes* (Persoon 1805; Rothmaler 1935; see also comments in Fröhner 1995b) because the stamens are extrorse and inserted at the inner side of the discus. The presence of at least 2 to rarely 3 or 4 extrorse stamens (in single flowers) and 1 to 12 stigmas (Figure 1), however have been considered sufficient to justify generic rank by various authors (Rydberg 1908; Rothmaler 1937; Gaviria 1996; Romoleroux 1996).

Subdivision of *Lachemilla* has differed between the most influential treatments (Table 2) especially those of Perry (1929) and Rothmaler (1937). Both recognised six units (series/sections) and divided one of them (*Aphanoides*) into five subunits (subseries/subsections) based on growth form, leaf characteristics or inflorescence structure. The two authors further agreed in defining two monotypic groups, *Polylepides* and *Diplophyllae*. Perry (1929) placed the remaining species in the four series. Rothmaler (1937) however arranged these species in three different sections and created the new monotypic section *Fruticulosae,* which he described from the type material, the only known collection (Puebla, Mexico) and which is probably extinct. The holotype of *Fruticulosa* has been destroyed at B and only a small fragment at JE is preserved, therefore the status remains unclear, but affinities seem to be with to *Aphanes* rather than *Lachemilla* (Romoleroux, pers. obs.). To our knowledge no work has been done on the extent or type of apomixis in *Lachemilla* nor has the ploidy level been assessed.

Here we present the first comprehensive molecular phylogenetic analysis of *Alchemilla* sensu lato (*Alchemillinae*; including *Aphanes* and *Lachemilla*). A major goal is to provide new evidence from nuclear and chloroplast genes on higher-level relationships within the clade. With these new phylogenetic results, we evaluate relative support from genes and morphology for currently recognised genera, and establish an initial framework that can be used for future investigations of relationships, biogeography and the evolution of autonomous agamospermy.

Table 2: Important contribution to the infrageneric classification of *Alchemilla*.

	infrgeneric classification of Eurasian and African *Alchemilla* species
Thunberg 1794	*A. capensis* is mentioned as first *Alchemlla* species from Africa (formal desciption 1823).
De Candolle 1825	*A. capensis* is mentioned within the section *Alchemilla,* no further devision of the section.
Rothmaler 1935	*Alchmilla* is devided into seven sections; African *Alchemilla* material in five sections and Eurasian material in two sections: section *Brevicaules* (including subsect. *Alpinae* and subsect. *Vulgares*) and section *Pentaphyllea*.
Haumann et Balle 1936	All african *Alchemilla* species are placed in subg. *Eualchemilla* (not differentiated in sections).
Rothmaler 1937	Recircumscribtion of the five African *Alchemilla* sections (sect. *Longicaules* including material from *Lachemilla* and possibly *Aphanes*). The Eurasian material in sect. *Pentaphyllea* and sect. *Brevicaules* (including material from Australia and Africa but mentioned with questionmarks).
Fröhner 1995	*Alchmilla* is devided into eigtheen sections: African *Alchemilla* sections are recognised according to Rothmaler 1937 and Eurasian taxa are grouped in four main and nine intermediate sections.
Notov 2004	African *Alchemilla* material in five sections and Eurasian material in two sections: section *Brevicaules* (including subsect. *Chirophyllum*, *Heliodrosium* and *Calycanthum*) and section *Pentaphyllea*.
	infrgeneric classification of *Lachemilla*
Mutis ex L. f. (1781)	*Lachemilla aphanoides* is first described as *Alchemilla aphanoides*.
Focke 1888	*Lachemilla* is mentioned as a seperate section for the first time.
Lagerheim 1894	*Lachemilla* is divided in two sections, sect. *Fockella* and sect. *Eulachemilla.*
Rydberg 1908	*Lachemilla* and *Zygalchemilla* are recognised as seperate genera.
Perry 1929	The genus *Lachemilla* is divided in six series (ser. *Aphanoides*, ser. *Polylepides*, ser. *Diplophyllae*, ser. *Nivales*, ser. *Obiculatae* and ser. *Pinnatae*)
Rothmaler 1937	The genus *Lachemilla* devided in six sections (sect. *Polylepides*, sect. *Rupestres*, sect. *Procumbentes*, sect. *Aphanoides*, sect. *Fruticulosae* and sect. *Diplophyllae*)
Notov 2004	The genus *Lachemilla* is devided in six sections according to Rothmaler.

MATERIAL AND METHODS

Phylogeny reconstruction in systems with apomixis, hybridisation and polyploidy

Apomixis influences the evolution of both genetic and morphological variability. The source of genetic variability in agamosperms is mainly derived from somatic mutations and recombination (Shi et al. 1996), or is present because of backcrossing, facultative meiotic recombination and cross-fertilization, as well as the multiple hybrid origins of apomicts from genetically divergent, usually diploid sexual ancestors (Hörandl 2004). Nevertheless, the morphological and genetic diversity within species in a predominantly apomictic system is usually much lower than that of their sexually reproducing relatives (Asker and Jerling 1992; Shi et al. 1996; Richards 2003). We might therefore expect that the amount of genetic variation and number of informative characters in DNA markers used in molecular phylogenetic analysis would be lower in apomictic species. However, almost all apomictic species, arguably including all species of *Alchemilla*, are of polyploid origin and have an enhanced rate of molecular evolution (Mogie 1992). Notwithstanding, several studies have shown that molecular markers such as ITS, *trn*LF or *mat*K, can be used to study evolutionary relationships within genera with apomictic lineages (Alice and Campbell 1999; Wittzell 1999; Kirschner et al. 2003; Fehrer et al. 2007).

Taxon sampling

Sampling of the species followed the strategy to (1) include the generic and subgeneric types of *Alchemilla*, *Aphanes* and *Lachemilla;* (2) include at least two representatives of each section (sensu Rothmaler 1935 1936-1937; Fröhner 1995a; Fröhner 1995b and Notov and Kusnetzova 2004), if possible these should include the type species and a second representative (3) species should represent the whole geographical and (4) the morphological range of the genus. With respect to the representation of taxonomic groups as described in point two, the material is complete except for *Aphanes* and two of Rothmaler´s (1937) sections of *Lachemilla,* i.e. *Fruticulosa* and *Polylepis,* for which fresh material was not available. Extraction from herbarium material proved difficult or impossible. Identification of *A. japonica* material that was provided by the Botanical Garden in Göttingen is uncertain as *A. japonica* in culture has been found to be a Caucasian species related to *A. speciosa* (P. Frost-Ohlsen pers. comm.). Outgroup sampling represents most genera in the Fragariinae-clade (Eriksson et al. 2003) and members of Potentilleae and other Rosoideae to test the monophyly of the genus and for rooting purposes. For some widespread and critical species, more than one accession was sequenced, but in most cases sequences proved identical and only one of them was used for phylogenetic reconstruction. Altogether 100 taxa were included in the final analysis (Table 4).

DNA extraction, sequencing and alignment

Different protocols for DNA extraction and amplification were applied in the respective labs of the collaborating authors. At the Institute for Systematic Botany of the University of Zurich, silica dried material was homogenised using two glass beads in 2 µl reaction tubes in a Regget Machine 2 x 130 sec at full speed. DNA extraction was performed using DNeasy extraction kit (Qiagen), following the manufacturer's instructions with minor modifications. Samples where diluted 1:100 in ddH_2O prior to Polymerase chain reactions (PCR) that were performed in 25 µl reactions (1 x PCR buffer, with 2.5 mM $MgCl_2$, 0.25 mM dNTPs, 1.6 µM primer and 1 unit of *Taq* polymerase (Sigma-Aldrich, USA) in a Biometra Thermocycler TGradient (Biometra, Göttingen, Germany). The entire ITS1-5.8S-ITS2 region and the *trnL-F* intergenic spacer together with the *trnL* intron were amplified and sequenced as described in Eriksson et al. (2003) with the exception that in Zurich PCR products were purified using DNA band purification kit (Amersham Biosciences, Otelfingen, Switzerland). Forward and reverse strand sequences were edited using Sequencher 4.2. (Genecode Corp.).

At Munich, total DNA was extracted from both silica gel dried and herbarium material as described earlier (Bräuchler et al. 2004) using the Macherey-Nagel Nucleo Spin Plant Kit. Standard protocols for PCR did not yield any product for either herbarium or silica gel dried material. Therefore, a different approach using Phusion™ high fidelity polymerase (Finnzymes, Finland) was used. PCR were performed following manufacturer's protocol with the following cycle profile: 1' of initial denaturation at 98°C, 35 cycles of 30'' at 98°C, 30'' at 53°C, 45'' of 72°C and a final extention for 10' at 72°C. The same primers as above were used and for trnL-F additonally the primers D and E (Taberlet et al. 1991). PCR products were purified using Microcon YM 100 filter devices (Millipore, USA), sequencing was performed using the Amersham Kit (Amersham, Freiburg) and an ABI 377 automated sequencer. Sequences were edited using GeneDoc (Nicholas and Nicholas 1997).

At the Department of Botany, Stockholm University, 0.02-0.03 g of silica gel dried or herbarium material was homogenised using a mini-beadbeater (Biospec products). Total DNA was extracted through a downscaled version of the CTAB protocol described by Doyle and Doyle (Doyle and Doyle 1990). In PCR reactions of 25 µL we used 1x Buffer, 1.5 mM MgCl2, 0.2 mM of each dNTP, 0.04% BSA, 0.3 µM of each primer, 0.5 units of Taq polymerase (Roche Applied Science, Germany), and 1 µL of DNA. PCR reactions were amplified in an Eppendorf Mastercycler gradient. Amplification products were cleaned using Montage PCR96 plates (Millipore) and a vacuum manifold. Base callings were obtained by using phred (Ewing et al. 1998, Ewing and Green 1998) and assembled with phrap (Green 1996) integrated in the Staden package (Staden 1996) under GNU/Linux.

Data matrices were aligned by eye, poly A or poly A/T regions were excluded from the trnLF dataset (9bp between 497-505 and 5 bp between 834-838). Gaps were coded by hand using the simple indel coding of Simmons and Ochoterena (2000).

Parsimony analyses (MP)

Datasets were analysed in three different ways (1) ITS and trnL-trnF regions separately, (2) separate subdivisions of this data, partitioned into ITS1, ITS2, trnL intron and trnL-trnF intergenic spacer (IGS) (the 5.8S, trnL and trnF exons were not analysed separately due to their lack of parsimony informative characters), (3) all data combined. Maximum parsimony analyses were performed using PAUP* version 4.0b10 (Swofford 2001) using heuristic searches with 1000 replicates of random addition sequence, tree-bisection-reconnection (TBR) branch swapping, MULTREE on (keeping multiple, equally parsimonious trees), saving a maximum of 50 trees each replicate. Support was assessed using 1000 replicates of non-parametric bootstrap analysis (Felsenstein 1985).

Potential incongruence between datasets was assessed visually (i) by comparing phylogenies from individual datasets and (ii) by comparing the robustness and resolution of phylogenies from combined data versus individual gene regions. There are two well-supported incongruences between the gene trees within the Eurasian Alchemilla-clade (Figures 4 and 5). It has been argued that in cases where incongruence is localised to particular taxa, or to specific areas of a tree, pruning of the conflicting taxa or clades may permit the datasets to be combined for analysis (Barber et al. 2007). Therefore taxa with incongruent gene phylogenies (*A. angustata* and *A. decumbens*), were removed and the remaining dataset reanalysed (termed here "combined analysis").

Bayesian inference

Bayesian analysis was performed as implemented in MrBayes 3.1.2. (Huelsenbeck and Ronquist 2001). Applying the Akaike Information Criterion using MrModeltest (Nylander et al. 2004) based on Modeltest (Posada and Crandall 1998), the general time reversible GTR model with gamma distributed rates was identified as best fitting the sequence data of ITS1, ITS2 and trnLF. For the 5.8S, SYM+G was identified as the best fitting model and GTR+G+I as the best model in the combined dataset. Bayesian analysis was carried out for each of the partition sets including the coded gaps. GTR+G+I was then used in the combined Bayesian analysis, and the parameter values of the different partitions were allowed to vary independently. For each partition, four chains (three hot, one cold) were run in two parallel runs for 2,000,000 generations for the separate analysis and 3,000,000 generations for the combined analysis, each sampling every 1,000 generations. The burnin was set to 100 tree or 100,000 generations for each run of the separate analyses and 200

trees or 200,000 generations for each run of the combined analysis (determined empirically from the log-likelihood values using Tracer; Rambaut and Drummond 2003-2007). A combined consensus tree of the last 3802 tree or 5602 trees respectively was constructed and clade credibilities for the bipartitions recorded as a measure of node support.

RESULTS

The length of the ITS sequences included in the final data matrix was very uniform around 624 bp. The aligned matrix including outgroups consisted of 665 bp, including 299 variable bp of which 208 bp were parsimony informative in addition to 14 parsimony informative characters from the indel-coding. The length of the *trn*LF sequences ranged from 643 to 853 bp. The aligned matrix consisted of 96 taxa with a total alignment of 1241 bp and 33 characters from the indel-coding, including 252 variable bp of which 134 bp were parsimony informative. A number of large indels were observed in the *trn*LF intergenic spacer (IGS). Unique insertions were observed in *A. pentaphyllea* (a duplication of 25 bp) and in *A. schizophylla* (28 bp); *A. kiwuensis* and *A. abyssinica* shared a identical insertion of 58 bp. There was a large deletion of 210 bp in *A. microbetula*, *A. roccatii* and *A. haumanii*. Topologies were unaffected when these indels were excluded from analyses (data not shown).

Four clades were retrieved in all analyses (Parsimony and Bayesian): *Aphanes*, Eurasian *Alchemilla*, African *Alchemilla* and *Lachemilla* with high (75-89) or very high (90-100) bootstrap support values as well as clade credibilities above 0.96 (Figures 4-6).

The Eualchemilla-clade

The monophyly of the Eurasian species of *Alchemilla* was well supported in all analyses. We will henceforth refer to this group as the Eualchemilla-clade. It comprises two major clades, which we will refer to as the Lobed-clade and the Dissected-clade. Most taxa in the Lobed-clade clade have lobed or not entirely dissected leaves, and most taxa found in the Dissected-clade have entirely dissected leaves (or nearly so), exeptions in the Dissected-clade are *A. angustata, A. decumbens, A. exigua, A. faeroensis* and *A. splendens*.

The monophyly of the Lobed-clade received high support values in the ITS and the combined analysis but low parsimony bootstrap support in the *trn*LF analysis. Resolution within the Lobed-clade is low due to the low sequence variability (6 bp in the *trn*LF dataset and 9 bp in the ITS sequence alignment within the reduced taxon sampling). *A. japonica,* the only sample of a East Asian *Alchemilla*, was in all analyses nested well within the Lobed-clade.

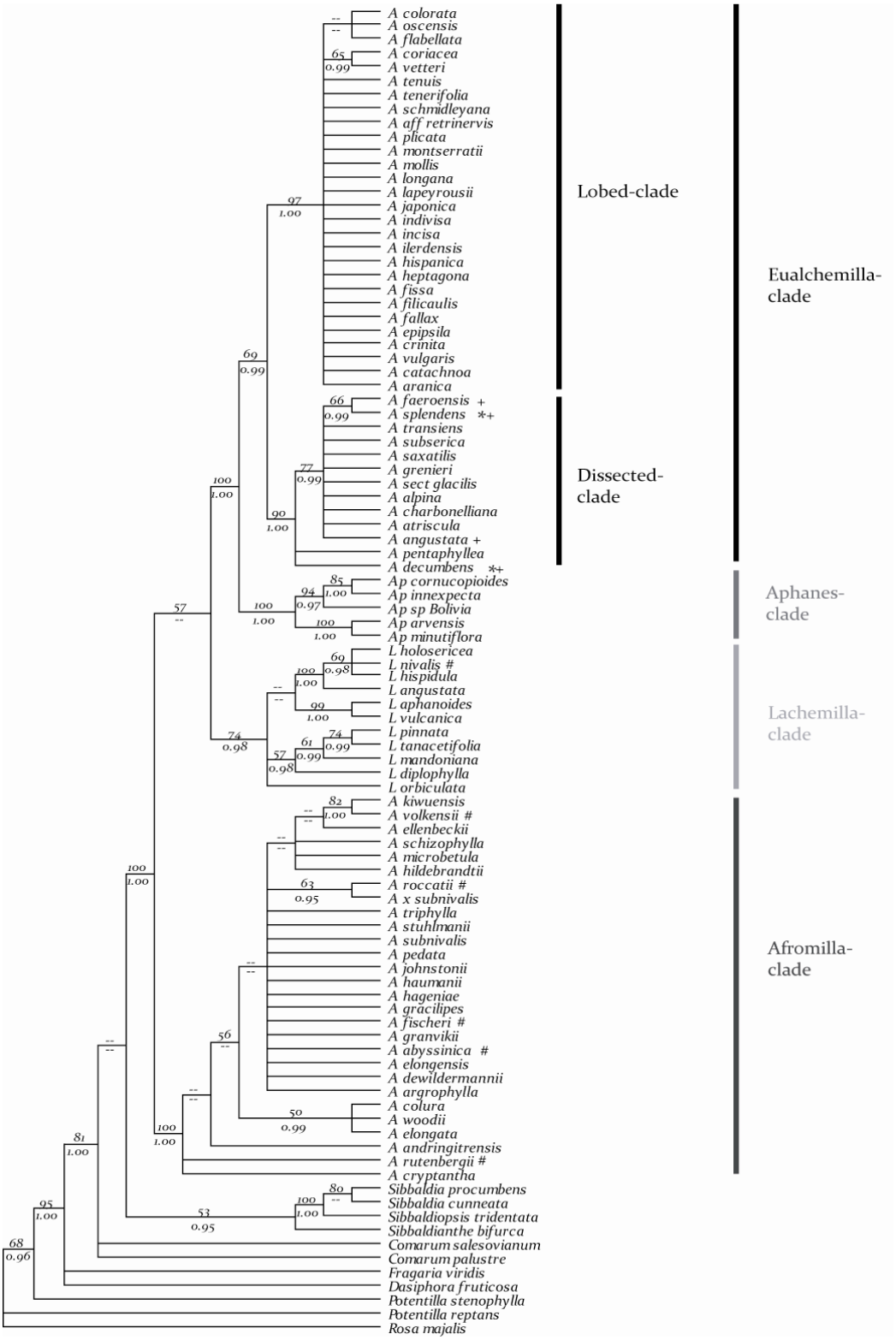

Figure 4: Strict consensus tree based on the nuclear ITS region reconstructed using Maximum Parsimony; Bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches. Asteriks indicate species that where removed from the dataset for the combined analysis because of incongruences between chloroplast and nuclear data. Hashes indicate species for which only nuclear sequences are present. Pluses indicate taxa placed in the Dissected-clade despite their lobed leaves.

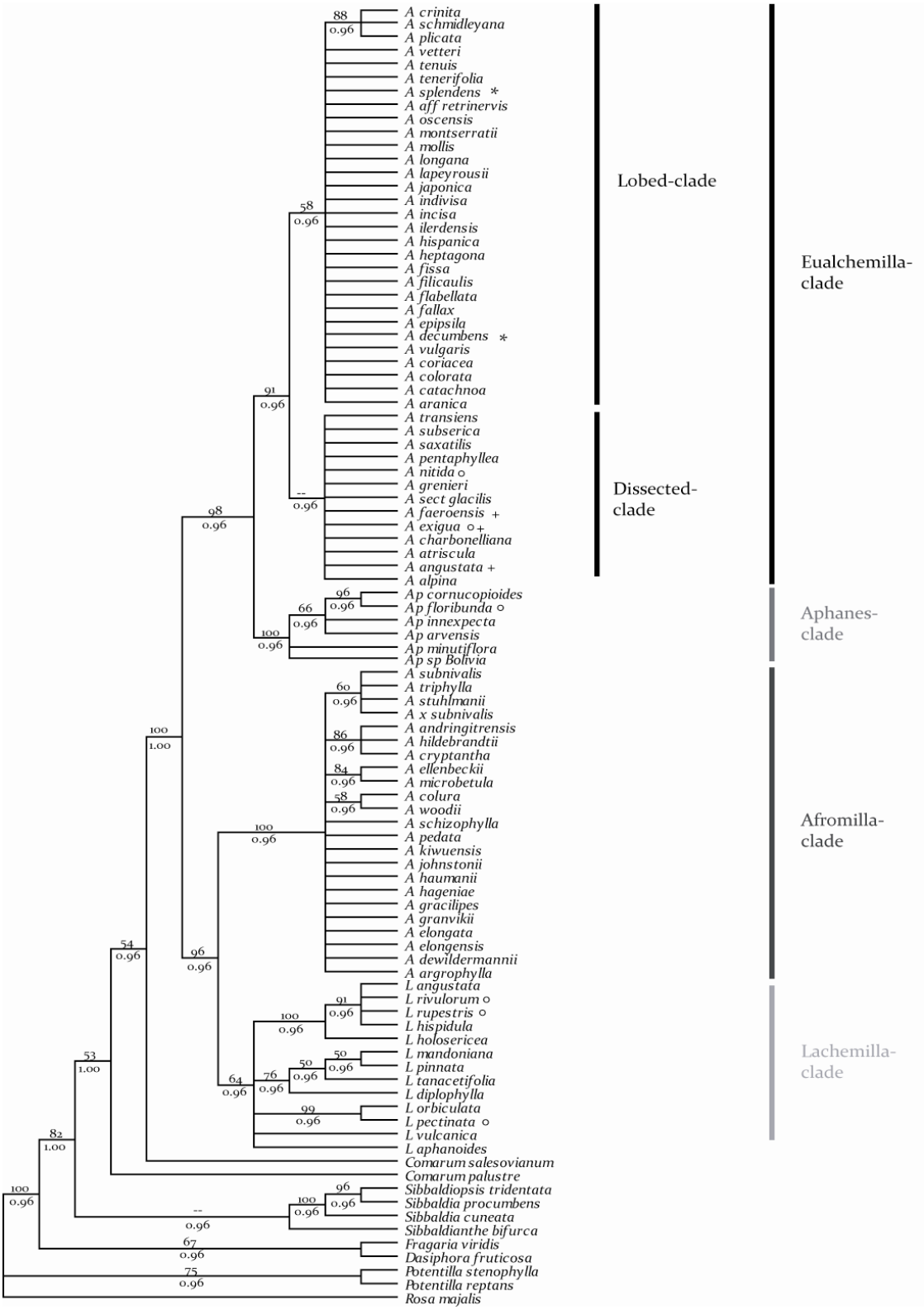

Figure 5: Strict consensus tree based on the chloroplast *trn*L-*trn*F region reconstructed using Maximum Parsimony; Bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches. Asteriks indicate species that where removed from the dataset for the combined analysis because of incongruences between chloroplast and nuclear data. Circles indicate species for which only chloroplast sequences are present. Pluses indicate taxa placed in the Dissected-clade despite their lobed leaves.

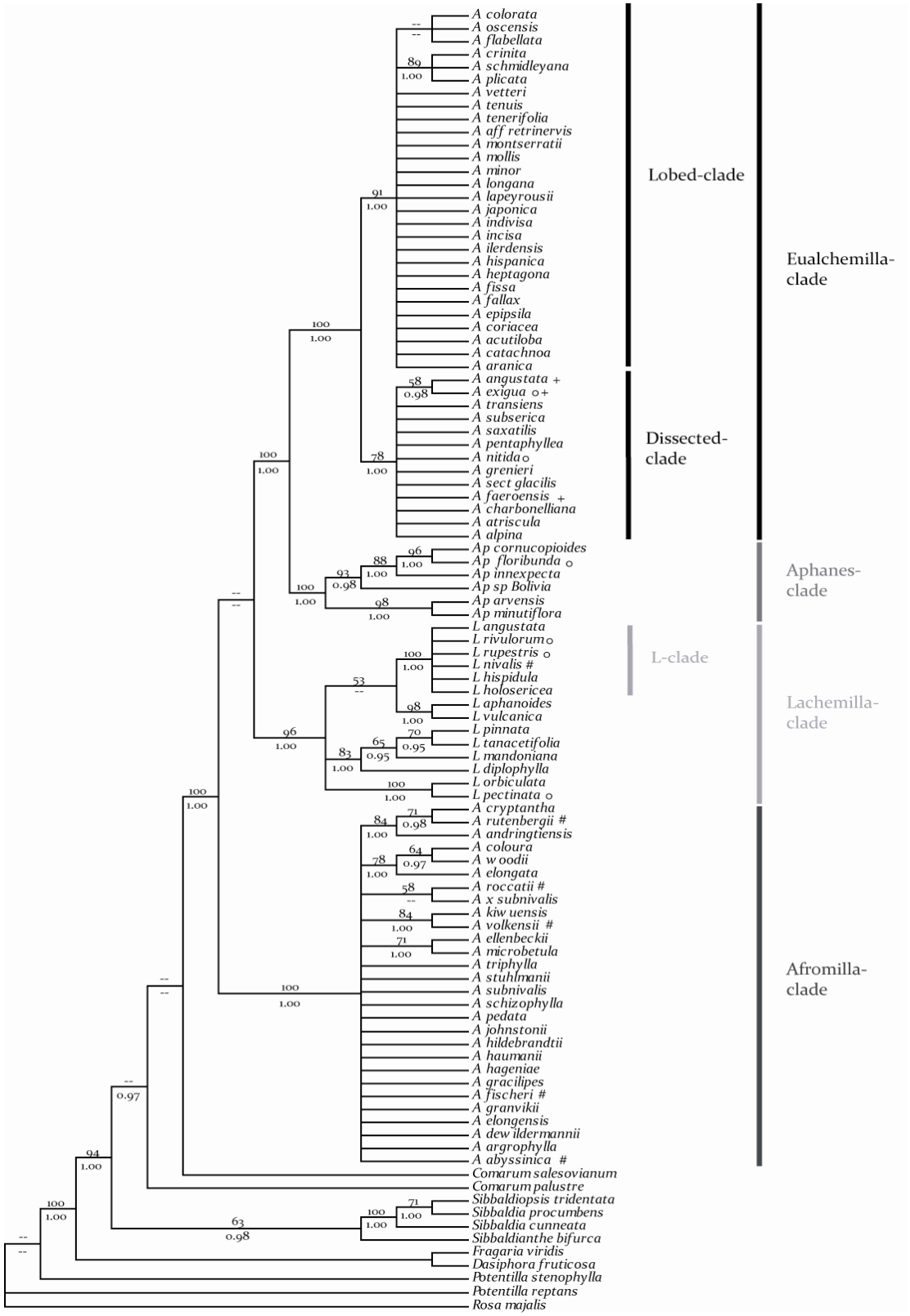

Figure 6: Strict consensus tree based on the combined dataset reconstructed using Maximum Parsimony; Bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches. Circles indicate species for which only chloroplast sequences are present. Hashes indicate species for which only nuclear sequences are present. Pluses indicate taxa placed in the Dissected-clade despite their lobed leaves.

The monophyly of the Dissected-clade also received high support values in the ITS and the combined analysis and low parsimony bootstrap support in the *trn*LF analysis. *A. pentaphyllea* was retrieved together with *A. decumbens* in the *trn*LF analysis as sister to the other members of the Dissected-clade and alone as sister to other members of the Dissected-clade in the combined Baysian analysis. However, this relationship collapsed in the strict consensus of the combined MP analyses. The Resolution within the Dissected-clade was low with some support for a sister species relationship between *A. saxatilis* and *A. transiens*. In the separate MP analyses of chloroplast and nuclear ITS data, *A. decumbens* and *A. splendens* were placed in the Lobed-clade (according to *trn*LF), and in the Dissected-clade (according to ITS) (marked with asterisk in Figures 4 and 5). *A. faeroensis* and *A. angustata* were in both the *trn*LF and the ITS analyses placed well within the Dissected-clade despite their lobed leaf morphology (marked with pluses in Figures 4-6). *A. nitida* and *A. exigua* were placed in the *trn*LF analysis in the Dissected-clade but ITS data is missing (marked with circles in Figures 5 and 6). The combined analysis yields high support values with respect to the monophyly of the Dissected-clade but no support within the clade (Figure 6).

The Afromilla-clade

A strongly supported clade including all the African *Alchemilla* species was received in all analyses. We will henceforth refer to this as the Afromilla-clade. The 29 taxa included in the analysis represent 50%-80% of all species that occur in Sub-Saharan and southern Africa (depending on the number of species recognised). These represent all recognised sections of *Alchemilla* in Africa, their full geographical distribution, all life forms, and a broad range of ecological preferences and morphological variation. Within the Afromilla-clade the number of variable characters is low and therefore neither the topologies of the gene trees nor of the combined analysis are well resolved. Even though the resolution within the Afromilla-clade is low, there seems to be some support for patterns in distribution and life form: All taxa from southern Africa (*A. colura*, *A. woodii* and *A. elongata*) form a clade with moderate support values at least in the combined analysis. Some of the accessions from Madagascar (*A. andringitrensis*, *A. cryptantha* and *A. rutenbergii*) form a well supported clade in the combined analyses and form a clade with low support in the combined Bayesian analyses together with the other accessions from Madagascar (*A. schizophylla* and *A. hildebrandtii*; data not shown). The third supported clade is a clade of *A. kiwuensis* and *A. volkensii*. A sister-group relationship between *A. kiwuensis* and *A. volkensii* is supported in the ITS and combined analyses, data for the *trn*LF region are missing. Two more clades with low to moderate support values in the combined analysis are present, one comprising *A. ellenbeckii* and *A. microbetula* and another comprising the two dwarf shrubs *A. roccatii* and an hybrid of *A. subnivalis*.

The Aphanes-clade

A clade including all the sampled species of *Aphanes* (the Aphanes-clade) was well supported in all analyses (100 bootstrap and 1.00 c.c., with exception of the 0.96 c.c. in the *trn*LF analysis). It is sister to the Eualchemilla-clade. The small Mediterranean *Ap. minutiflora* was well supported as sister to the widespread Eurasian *Ap. arvensis* in the ITS and the combined analyses, whereas this is contradicted in the *trn*LF analysis, however not strongly supported. The South American species form a clade together with the more robust *Ap. floribunda*, again only in the ITS and the combined analyses. *Ap. bachitii* (from Ethiopia) and *Ap. parodii* (from South America), which have been hypothesised to be the most basal members of the clade based on their morphology, were not included in the analyses due to the lack of material and/or difficulties in PCR amplification. Further conclusions on the geographical origin of this clade will have to await denser taxon sampling.

The Lachemilla-clade

The Lachemilla-clade was supported with moderate to high values in the separate analyses and support was increased considerably in the combined analysis. The clade was sister to the Afromilla-clade in the *trn*LF-analysis and sister to a combined Aphanes- and Eualchemilla-clade but with very weak support in the ITS analysis. It is notable that the support for the clade comprising the Lachemilla-clade and the Afromilla-clade decreased in the combined analysis. This indicates a conflict in the data, not just a lack of resolution in the ITS data. Combining the datasets did not result in improved resolution in this part of the topology. *Lachemilla* showed the highest amount of sequence divergence within the analysed dataset which led to a better resolution within the clade, though this was weakly supported which might also be a result of the sparse taxon sampling. Four clades however seem to be more reliable and are retrived in all analyses (where sequence information was present). One comprises *L. pectinata* and *L. orbiculata,* a second with four species, within which *L. diplophylla* is sister to a clade including *L. mandoniana*, *L. pinnata* and *L. tanacetifolia*, a third contains *L. aphanoides* and *L. vulcanica* and the fourth contains *L. holosericea, L. nivalis* and four others.

DISCUSSION

The results of the molecular phylogenetic reconstruction were significant at a number of levels, despite incomplete resolution and some evidence for conflict between the data partitions.

Taxonomic implications

Pfeil and Crisp (2005) argue that "because there is no objective way to measure the degree of character similarity within a group of species, there is no phenetic criterion by which to decide whether to recognise a group of similar organisms as a genus, family or other rank". I.e. genera are essentially a matter of opinion. Generic revisions tend to focus either on clarification of membership of monophyletic groups deemed a priori to be genera, or on arbitrary re-classification of accepted monophyletic groups to generic rank. Three factors are considered to be of primary importance in making taxonomic (re-)classifications, especially on assigning generic rank: (i) monophyly combined with (ii) morphological synapomorphies and (iii) nomenclatural stability. Nomenclatural stability especially applies to genera (Pfeil and Crisp 2005, Scotland and Sanderson 2004) since in the binominal system a change in genus name consequently changes the names of all species within.

Circumscribing *Alchemilla* in the wide sense, including the four monophyletic groups Eualchemilla-, Aphanes-, Lachemilla- and the Afromilla-clade on a subgeneric or informal level fits all three mentioned criteria.

(i) Monophyly: Our analyses have shown that *Alchemilla* in the wide sense is monophyletic and nested within the subtribe Fragariinae (cf. Eriksson et al. 2003). It comprises four very well supported clades. If *Alchemilla* in the wide sense is recognised at the rank of genus, thus including the Eualchemilla-, Aphanes-, Lachemilla- and Afromilla-clades, then the principle of monophyly will be satisfied at all taxonomic levels. The same is not true for any other of the solutions discussed. If *Alchemilla* in the wide sense is recognised at the rank of subtribe (Alchemillinae), including the three genera *Alchemilla*, *Aphanes* and *Lachemilla*, both *Alchemilla* and the subtribe *Fragariinae* are paraphyletic, the latter because Alchemillinae is nested within Fragariinae. If four genera are recognised: *Alchemilla* (the Eualchemilla-clade), *Aphanes*, *Lachemilla* and "*Afromilla"* (African *Alchemilla* as a new genus), these are monophyletic but *Fragariinae* remains paraphyletic. Therefore, if the principle of monophyly is to be applied, it will be necessary to abandon the subtribe Alchemillinae and either apply the name *Alchemilla* in a broader sense, or to group its constituent species in four genera rather than three.
(ii) Morphological synapomorphies: *Alchemilla* in the wide sense as a monophyletic group can be recognised by floral synapomorphies: lack of petals and presence of two whorls of four calyx and four epicalyx lobes that form a hypanthium. (Figure 1). If Alchemillinae is recognised as a tribe including the four genera Eurasian *Alchemilla*, *Aphanes*, *Lachemilla* and "*Afromilla"*, then new diagnostic morphological characters have to be found to separate Eurasian *Alchemilla* from African "*Afromilla*". Notov and Kusnetzova (2004), worked extensively to assess the taxonomic delimitations within Alchemillinae. They did not report any characters on which it would be possible to separate the Eurasian from the African sections of *Alchemilla*. This is also the conclusion that we have reached, despite

having had the benefit of a robust phylogeny with which to focus investigation into the issue.

(iii) Nomenclatural stability: The classification of *Alchemilla* has undergone a number of changes (Table 1). We will here only outline the most important ones: *Alchemilla* was first described by Linnaeus (1753). The first groupings of species were presented by Buser (1892) in which he treated the Eurasian taxa only. His system was refined by Rothmaler (1934-37) and Walters and Pawlowski (1968) and corrected for the Eurasian sections by Plocek (1982). Hauman and Balle (1936) based their classification mainly on life forms, shoot type and leaf dissection but did not complete their work. Hedberg (1957) concluded from his study of the Afroalpine *Alchemilla* species that these taxa cannot be split into distinct micro-species and recognised five African and East-Asian Sections. Fröhner (1995a) revised the European species for Flora Europea and for the Flora Iberica (Fröhner 1998). Notov and Kusnetzova (2004) tried to unravel the taxonomic relationships in Alchemillinae by using architectural units. Most authors agree on recognising three different groups on a subgeneric or generic level (*Alchemilla*, *Aphanes* and *Lachemilla*), placing taxa from tropical and southern Africa in separate sections within *Alchemilla* based on biogeography, without describing diagnostic characters which would separate all African material from the Eurasian species. Thus they do not indicate that the African Alchemilla species represent a separate subgenus or genus distinct from an Eurasian Alchemilla subgenus or genus.

Aphanes was first described by Linnaeus (1753) on the basis of material of *A. arvensis*, but he misinterpreted the stamen that is inserted at the inner side of the discus as an additional stigma. Scopoli reunited *Aphanes* with *Alchemilla* in 1772, but Persoon resurrected *Aphanes* in 1805 after more species had been discovered in South America. De Candolle (1825) treated *Aphanes* again as a section of *Alchemilla* whereas Rothmaler initially treated *Aphanes* as a subgenus (1935) but changed his opinion in 1937 where he raised *Aphanes* and *Lachemilla* from the rank of subgenera to that of genera. Some authors have since followed his recommendation and treated them as separate genera, whilst others such as Kalkman (2004) have not.

Lachemilla was first described as a section of *Alchemilla* by Focke (1888). Lagerheim (1894) raised it to genus level, a view that was followed by Rydberg (1908) who additionally recognised the genus *Zygalchemilla*. Murbeck (1915) treated *Lachemilla* together with *Aphanes* again as a section of *Alchemilla*. The first revision of *Lachemilla* was conducted by Perry in 1929 who recognised 41 species in 6 series within the section *Lachemilla*. Rothmaler (1935) was the first to give *Lachemilla* the rank of a subgenus and then later revised this position and gave it genus rank again (Rothmaler 1937) creating 72 new combinations. More recently, authors like Gaviria (1996) and Romoleroux (1996) have used the rank of a genus in their regional treatments of *Lachemilla*.

It is our opinion, that recognising *Alchemilla* as a single genus will lead to greater stability whilst minimising taxonomic changes. Therefore, we prefer the principle of

monophyly to be given preference, and apply the name *Alchemilla* in a broader sense, rather than using *Aphanes*, *Lachemilla* and two separate genera of *Alchemilla* which cannot be distinguished on criteria other than their geographic distribution. If new characters are identified, which can be used as synapomorphies for the African clade, it might be that having four separate genera would be preferable. At this time, however, it seems that arguments for nomenclatural stability strongly support keeping all of these species in *Alchemilla*.

Robust phylogenetic hypothesis for Eualchemilla-clade?

The monophyly of the Eurasian species of *Alchemilla* was well supported and this group was very well supported as sister to the Aphanes-clade. Within the Eualchemilla-clade two subsections (Dissected- and Lobed-clade) are very well supported by the molecular phylogenetic reconstruction (Figure 6). Some of the earliest authors have proposed a differentiation between groups of species of *Alchemilla* in the strict sense on the basis of the level of dissection of their leaves. Especially noteworthy here is the classification-system proposed by Buser in 1892, which was refined by Rothmaler in 1934. Rothmaler recognised the section *Brevicaules* with the two subsection *Alpinae* (the Dissected-clade) and subsection *Vulgares* (the Lobed-clade) and subsequently gave *Pentaphylleae* the rank of a separate section. Later this distinction between subsections *Alpinae, Vulgares* and *Pentaphylleae* within the Eurasian *Alchemilla* was dropped and several other species groups were included at the same subsectional or sectional rank (Fröhner 1995a). The results of the molecular phylogenetic analysis are congruent with the earlier authors that proposed three subsections (*Alpinae, Vulgares* and *Pentaphylleae*) based on their morphology. However the sister species relationship of *A. pentaphyllea* to the rest of the Dissected-clade (section *Alpinae*) is not supported in the combined analysis and there are some exceptions of species with lobed leaves in the Dissected-clade (*A. decumbens* and *A. splendens* for one marker whilst the other marker places them in the lobed clade; *A. exigua,* for which only one marker is available and *A. angustata* and *A. faeroensis* for both markers). However, these taxa are from sections of putative hybrid origin (Table 3). All the examples in which morphology does not appear to agree with the molecular phylogenetic results indicated an incorrect placement of taxa with lobed leaves in the dissected clade. No taxon with dissected leaves was placed in the Lobed-clade in any of the analyses.

Table 3: Hybrid origin of sections according to Fröhner (1995a) for species with lobed leaves which were place in the Dissected-clade.

Species	**Section**	**Parental sections**	**Other species of the same section**
A. decumbens	sect. *Decumbentes*	*Ultravulgares* (Lobed-clade) and *Pentaphylleae* (Dissected-clade)	*A. tenuis*
A. splendens and A. faeroensis	sect. *Splendentes*	*Ultravulgares* (Lobed-clade), *Erectae* (Lobed-clade) and *Alpinae* (Dissected-clade)	A. *aranica, A. hispanica*
A. exigua	sect. *Plicatae*	*Ultravulgares* (Lobed-clade), *Alpinae* (Dissected-clade) and *Pentaphylleae* (Dissected-clade)	A. *colorata, A. filicaulis, A. plicata, A. schmidelyana*
A. angustata	sect. *Alchemilla*	*Ultravulgares* (Lobed-clade) and *Erectae* (Lobed-clade)	*A. crinita, A. ilerdensis, A. tenerifolia, A. vulgaris*

Biogeography of the Afromilla-clade

The strong separation of the African and the Eurasian *Alchemilla* species is a striking pattern that has not been postulated before. It is interesting to note that there seems to have been only a single dispersal between the two areas leading to two well supported monophyletic groups. Within the Afromilla-clade the genetic variability is higher than in the Eurasian Alchemilla-clade, which might be due to higher levels of sexual reproduction in these species as proposed by some authors on the basis of pollen viability (Hedberg 1957; Hedberg 1986; Fröhner 1995a). Functional pollen is unnecessary for plants that exhibit autonomous apomixis, which is supposed to be coupled with degenerative phenomena, such as meiotic disturbance, which may interfere with pollen formation. In the European sections of *Alchemilla* the pollen is aborted and seeds develops precociously (before anthesis) in the flower (Izmailow 1994; Fröhner 1995a). Hedberg (1957) suggested that the Afroalpine *Alchemilla* species might not be obligate apomictic, referring to high levels of pollen production in some of these taxa. However, this could reflect pseudogamous (rather than autonomous) apomixis, and therefore does not necessarily prove that they are not apomictic at all, or that they are facultative apomicts.

The resolution within the Afromilla-clade is low, with some support for patterns in distribution (represented by the two clades in southern Africa and Madagascar). Resolution is insufficient to allow meaningful reconstruction of ancestral states, and the lack of cytological data does not allow for the reconstructions of the role of polyploidy in the occupation of the Afrotemperate Regions. More variable markers or population-level molecular techniques would need to be applied to be able to make further inferences at this level of relatedness. For example, a population based analysis of the dwarf shrubs endemic to the Ruwenzori Mountain range might give more insights into the historical

development of the mountain chain that has so uniquely given rise to a number of co-occurring *Alchemilla* species.

Lachemilla-clade

This analysis represents the first assessment of monophyly of *Lachemilla*. Further research, however, including analysis of more species is needed to address questions of, natural subgroupings, biogeography and the migration history of *Lachemilla*.

Relationships within *Lachemilla* as revealed by our analyses are to some extent congruent with those based on morphological data. However, the taxon sampling is low, thus a more complete sampling might reveal other relationships. We will therefore give here only a single example were molecular data point towards a possible relationship not inferred from morphological data (marked as the L-clade in Figure 6). *L. rupestris* is nested here in section *Lachemilla* (which corresponds to series or section *Nivales* but in terms of nomenclature, the correct name should be *Lachemilla* as *L. nivalis* is the type not only of the section but also of the subgenus/genus), however its morphological characteristics do not support this. The section *Lachemilla* is highly supported in all analyses and corresponds well to the very characteristic leaf-morphology of this group, with the exception of the newly discovered relationship of *L. rupestris*.

Incongruences in the Eualchemilla-clade: hybridisation/introgression or incomplete lineage sorting?

Interspecific hybridisation, especially in case of allopolyploidy, is one of the most important factors leading to phylogenetic incongruence between loci of the plastid and nuclear genomes. The most extreme case is chloroplast capture, a process that can occur at a variety of taxonomic levels (Rieseberg and Soltis 1991), i.e. cpDNA introgression can occur in the absence of analogous nrDNA gene introgression. As a result, clustering taxa on the basis of chloroplast DNA can fail to correspond to taxonomic units, groups supported by analysis of morphological characters, or clades indicated by nuclear markers because either the chloroplast of these taxa is derived (captured) from another taxon (e.g., in *Heuchera* group (Saxifragaceae) Soltis and Kuzoff 1995; Veroniceae in Albach and Chase 2004; *Achillea* (Asteraceae) Guo et al. 2004; *Hieracium* (Asteraceae) Fehrer et al. 2007) or several independent chloroplast lineages are present in a single taxon (e.g. in *Hordeum* (Poaceae) Jakob and Blattner 2006).

In the Eualchemilla-clade, and possibly in all taxa of *Alchemilla*, recent hybridisations are thought to be extremely rare due to their reproduction via autonomous apomixis and the absence of diploids (Fröhner 1995a). However, hybridisation events are likely to have been more frequent in the past, when there were still diploid species present. In many other well researched groups with abundant apomictic reproduction

such as *Hieracium* (Fehrer et al. 2007), *Rubus* (Alice and Campbell 1999), *Taraxacum* (Kirschner et al. 2003) or the *Ranunculus auricomus* complex (Hörandl 2004; Hörandl et al. 2005) hybridisation, facultative apomixis and introgression, as revealed by incongruent gene phylogenies, has been hypothesised as having played an important role in the evolution of the groups. Therefore, we suggest that one possible explanation of the observed incongruence in the cpDNA and nrDNA data in the Eualchemilla-clade is due to hybridisation/introgression including cpDNA haplotype capture. All species with incongruent placement in the Lobed- or Dissected-clade have previously been placed in putative hybrid sections based on their morphology (Table 3). The observed placement of taxa (*A. decumbens* and *A. splendens)* in the Lobed-clade for the cpDNA sequences and not the Dissected-clade (as according to the nrDNA) could then be interpreted as chloroplast capture as a result of hybridisation. However, it is interesting to note that not all members of putative hybrid sections show an incongruent pattern, and that multiple sequencing of different individuals of the same species resulted in identical sequences for both chloroplast and nuclear markers.

A second possible explanation of the observed data is incomplete lineage sorting, the persistence of ancestral polymorphisms through speciation events (Wendel and Doyle 1998; Linder and Rieseberg 2004; Jakob and Blattner 2006). In this, different copies of ITS can homogenise to either paternal or maternal copy, and thus hide hybrid origins (Alvarez and Wendel 2003) as possibly the case in *A. faeroensis* and *A. angustata*. This homogenisation, known as concerted evolution, arises through mechanisms such as unequal crossing over and high-frequency gene conversion (Alvarez and Wendel 2003). Therefore concerted evolution can only occur given meiosis. In Eurasian *Alchemilla* the central nucleus is formed without meiosis from unreduced egg cells or somatic cells and the embryo is produced pathenogenetically (without fertilisation). Thus it is asummed that in most members of Eurasian *Alchemilla* meiosis is circumvented, an assumption that is further supported by the high level of ploidy in combination with a relatively frequent occurrence of uneven number of chromosomes (Asker and Jerling 1992). Lack of meiosis would effectively halt the processes of concerted evolution. A possible alternative explanation might be that meiosis is not always interrupted completely. As we have no reliable measurements of the level of meiosis that occurs in *Alchemilla*, it is difficult to estimate whether the observed incongruence is an artefact from the time when *Alchemilla* was reproducing sexually and that hybridisation has given rise to such a large number of lineages or microspecies, or whether there is an ongoing process of faculative sexual reproduction or meiotic processes in the formation of the egg cell.

CONCULSION AND FUTURE RESEARCH

We provide here the first molecular phylogeny of the Alchemillinae. Four distinct clades are revealed: the Eurasian Alchemilla-clade, Aphanes-clade, Lachemilla-clade and the African Afromilla-clade. We suggest treating *Alchemilla*, *Aphanes* and *Lachemilla* as a single genus *Alchemilla,* based on the lack of evident characters for the identification and description of the Afromilla-clade at the rank of genus (without which *Alchemilla* would be rendered paraphyletic with respect to *Aphanes* and *Lachemilla*) and nomenclatural stability, because relatively few new combinations will have to be made.

Future research might reveal still more complex patterns in the evolution of *Alchemilla*. Sampling of many individuals and possibly cloning for multiple haplotypes may be necessary to confirm the basic patterns presented in this paper. Species relationships within the clades remain largely unresolved due to low genetic variability and possible recent speciation. Different molecular techniques or markers such as AFLPs or ISSRs, or more variable genomic regions may have to be applied to be able to resolve relationships at this level of relatedness. Taxonomic implications from this study, corroborated by partial revisions and cytological investigations of *Lachemilla* and a revision of *Aphanes* are in preparation and shall be presented elsewhere.

CHAPTER 4:

Synopsis of sub-Saharan and African *Carex* L. (Cyperaceae)

Berit Gehrke

Manuscript for Adansonia

ABSTRACT

This synopsis provides a key, synonymy, habitat descriptions, and distributions for the 83 species and five additional infraspecific taxa of *Carex* known from Tropical and Southern Africa and Madagascar. It is the first treatment of *Carex* including all Tropical and southern temperate areas since Kükenthal's monograph of the subtribe Cariceae in 1909.

Keywords: Taxonomy; species keys

INTRODUCTION

The genus *Carex* (Cyperaceae; Cariceae) was first described by Linnaeus (1753). It currently comprises about 1600-2000 species (Kubitzki 2004), making it one of the largest genera of vascular plants. It has an almost worldwide distribution with highest species numbers in Eastern Asia and North America. The last comprehensive treatment of *Carex* in Africa dates back to Kükenthal's monograph of the subtribe Cariceae in 1909. Subsequent descriptions of new taxa and regional taxonomic treatments have led to inconsistencies in species delimitations and confusion regarding the identification of specimens and correct application of names. The synopsis presented here is intended to summarise the scattered literature on *Carex* in Africa, including notes on the taxonomic status of species as appropriate and a comprehensive key for all species of *Carex* from Tropical and Southern Africa and Madagascar.

Morphology, ecology and distribution of *Carex*

Carex species are perennial, rhizomous, mostly wind-pollinated, self-compatible, monoecious (rarely dioecious) herbs. The leaf blades are usually V- or M-shaped in cross section. All species have terminal inflorescences composed of one or several (pseudo-) spikelets arranged as spikes, racemes or panicles. The bracts subtending the (pseudo-) spikelets are leaf-like or scale-like. The perianth is absent. Flowers are always unisexual. The staminate florets consist only of 1–3 stamens. They are subtended by a scale (i.e. staminoid scale). The pistillate florets are enclosed by a bract with fused margins (called a utricle or perigynium). The utricle opens only at, or near to, the apex. The inflorescence axis extends into the utricle and is referred to as the rachilla. In most *Carex* species the rachilla is reduced and inconspicuous. The pistillate florets are also subtended by a scale-like bract (i.e. the pistillate scale). Staminoid and pistillate scales are usually similar but can differ in size, shape and colour. In older literature these scales are referred to as glumes. The style is 2–3(–4)-fid (i.e. has 2-3(-4) branches). Achenes are biconvex, plano-convex, or trigonous, rarely 4-angled (Smith & Faulkner 1976; Timonen 1993; Vegetti 2002). *Carex* can form tussocks or stands of tufted individuals, or develops into mats.

Carex species are most commonly found in temperate areas and with the exception of a few species in Southeast Asia and Africa are absent from most tropical lowlands. Some species occupy large distributional ranges, for example circumpolar bipolar (Moore & Chater 1971; Vollan 2006). *Carex* species are commonly associated with moist to wet habitats in which they are often dominant or co-dominant. However, the genus is also common in drier habitats such as montane grasslands, montane rocky habitats, and forest understory (Ball & Reznicek 1997) and is common in tropical alpine areas (Smith & Cleef 1988).

Classification

Inflorescence organization was one of the more important characters used by Kükenthal (1909) to define subgenera in *Carex*. His revision of the subtribe is still the most recent and most widely referenced monograph. Kükenthal divided *Carex* into four subgenera: *Primocarex, Vignea ,* (*Eu-*) *Carex* and *Indocarex*. This classification has been criticized, particularly regarding subgenus *Primocarex* (which is then referred to as section *Psyllophora* F. Muell.) and subgenus Indocarex (also known as section *Vigneastra* Tuck.). Kükenthal's classification is nevertheless still widely accepted with some modifications (Smith and Faulkner 1976; Egorova 1999; Reznicek 1990).

Phylogeny

Recent investigations of the genus and related genera using DNA sequences have both clarified and confused the classification and phylogeny of the genus. All investigations have confirmed the monophyly of subgenus *Vignea* (Yen & Olmstead 2000; Ford *et al.* 2006; Roalson et al. 2001; Waterway & Starr 2007). Subgenus *Carex* is probably paraphyletic and probably includes subgenus *Indocarex* (Roalson et al. 2001; Waterway & Starr 2007) which has been found to be either paraphyletic (Roalson et al. 2001) or monophyletic (Waterway & Starr 2007; Gehrke & Linder, unpubl. data). The bulk of subgenus *Primocarex*, together with *Cymophyllus, Uncinia*, *Kobresia and Schoenoxiphium* plus a few species of subgenus *Carex*, form a paraphyletic group (Starr *et al.* 1999; Starr *et al.* 2004; Waterway and Starr 2007). Molecular phylogenetic investigations differ in their placement of subgenus *Vignea*; some place it as a sister group to subgenus *Carex*, while others place it as a sister group to the whole of the tribe Cariceae (Ford *et al.* 2006).

Carex in sub-Saharan Africa

Carex is considered to be poorly represented in sub-Saharan Africa (Ball 1990; Reznicek eflora North America) especially compared to the species rich temperate areas of the Northern Hemisphere. Approximately 80 species are currently recognised. A number of authors contributed descriptions of species and taxonomic treatments of taxa from Tropical and Southern Africa: we will briefly introduce the most important ones. Among the first to publish widely on African Cariceae was C.B. Clarke (1902) who wrote the section on *Carex* for the Flora of Tropical Africa and carried on working on the genus (1902b). Durand (1894) published an extensive synopsis in the Conspectus Florae Africnae. Schumann included a smaller number of new species in the book of Engler (1895) on plants from East Africa. Kükenthal (1909) was the last to include all African *Carex* species known at that point as a part of his taxonomic revision of the subtribe Cariceae. Nelmes (1937; 1938a, b; 1939; 1955) published a number of new species and discussions of existing African *Carex* species but did not publish keys or a single reference summary of his work.

Chermezon (1932) focussed only on material from Madagascar, while Haines and Lye (1983) revised only the East African material, which is currently being revisited by Verdcourt for a forthcoming volume of the Flora of East Africa (pers. com.). A few South African species were summarised in Gordon-Grey (1995).

Problems in species identifications

Species identification is often problematic in *Carex*. Often only well developed material with full sized and mature utricles can be identified with confidence, especially for those unfamiliar with the group.

Problems arise mainly because of:

- Morphological variation throughout the ontogeny of an inflorescence resulting in:
    - different appearance of the spikelet at anthesis and during fruiting
    - different appearance inflorescence after anthesis, sometimes even after fruiting
    - differences within one spikelet between terminal and distal parts (especially in subgenus *Indocarex*)
- Variation in the distribution of male and female parts especially within one spikelet. For example in subgenus *Carex,* in which male and female florets are clearly separated, a few male florets can appear on the terminal or distal part of otherwise strictly female spikelets or *vice versa*.
- The occurrence of shorter spikelets at the base of usually unbranched spikelets in subgenus *Carex* can lead to a very different appearance of the inflorescence.

Aim of the synopsis

The synopsis presented here is intended to summarise the scattered literature on *Carex* in Africa, including assessment or at least some notes on the taxonomic status of species as appropriate. A comprehensive key for all species of *Carex* from Tropical and Southern Africa and Madagascar is included for the first time. A complete taxonomic revision of the genus is still needed, but in its absence this should serve as a guide for identification and correct nomenclature of *Carex* species in Africa. The results are based on extensive study of literature and also includes data from the Monocot Checklist (http://www.kew.org/wcsp/monocots/) and African Flowering Plant Database (http://www.ville-ge.ch/cjb/bd/africa/index.php) and of herbarium material from collections at major herbaria in Europe (BM, E, G, K, M, P, S and Z+ZT) and in Africa (BOL, EA, ETH, DAR and PRE) plus types represented in the ALUKA database (http://www.aluka.org/page/content/plants.jsp). Where appropriate, it takes into account the results of molecular phylogenetic analyses, in particular as published by Gehrke and Linder (submitted). Only synonyms based on African types, or referred to in the African literature, are listed.

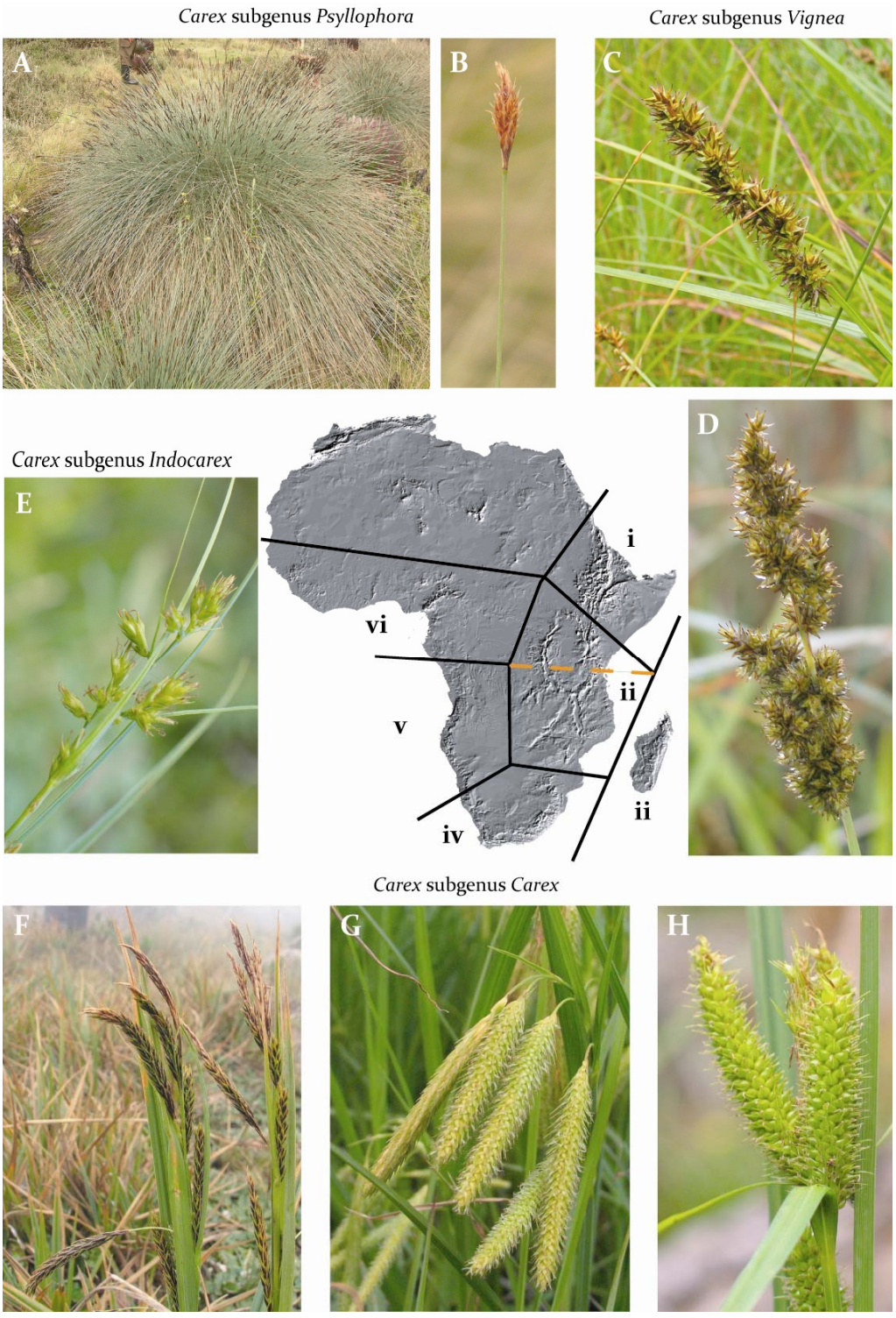

Figure 1: A-B *Carex* subgenus *Primocarex*: **A)** Tussock of *C. runssoroensis*, Uganda, Rwenzori Mts.; **B)** *C. monostachya*, Kenya, Mt. Kenya; **C-D** *Carex* subgenus *Vignea:* **C)** *C. erythrorrhiza,* Ethiopia, Bale Mts. **D)** *C. lycurus*, Malawi, Nyassa Plateau **E)** *Carex* subgenus *Indocarex: C. brassii,* Malawi, Zomba Plateau **F-H)** *Carex* subgenus *Carex:* **F)** *C. simensis*, Kenya, Aberdare Mts. **G)** *C. austro-africana,* South Africa, Drakensberg Mts. **H)** *C. sphaerogyna*, Madagascar, Ankaratra Mts. **i-vi** division of Africa as mentioned in the key **i)** North-eastern Africa **ii)** East Africa (divided in Northern and Southern East Africa) **iii)** Madagascar **iv)** Southern Africa **v)** South-western Africa **vi)** West Africa

KEY TO CAREX SUBGENERA

(see also Figure. 1; *C. negrii*, *C. heterodoxa, C. hovarum* and *C. zuluensis* are not included in the key because of their uncertain placement)

1. Spikelet solitary, terminal ..... subgenus **PRIMOCAREX**
1* Spikelets several ..... 2.

2. Spikes usually bisexual, sessile, arranged in branched panicles, prophyll absent ..... subgenus **VIGNEA**
2* Spikes usually bisexual or unisexual, arranged in branched panicles of more or less pedunculate spikes, prophyll present but sometimes minute ..... 3.

3. Spikes unisexual or bisexual with male and female spikelets (florets) not interspersed,prophyll not inflated but scale like and often minute ..... subgenus **CAREX**
3*. Spikes bisexually arranged in branched panicles with a prophyll which resembles a utricle at the base of the inflorescence branch .. subgenus **INDOCAREX**

SUBGENUS PRIMOCAREX KÜK. / SECTION PSYLLOPHORA (Degl.) Peterm.

The subgenus *Primocarex* or section *Psyllophora* consists of 4 species and 1 variety in sub-Saharan Africa. The subgenus is polyphyletic, but easily distinguished: species assigned typically to this subgenus have an inflorescence which consists of a single terminal spike (Starr, Bayer & Ford 1999; Starr, Harris & Simpson 2004).

A REVISED KEY TO PSYLLOPHORA/PRIMOCAREX IN AFRICA

1. Terminal spike dense ..... 2.
1* Terminal spike loose, single spikelets distant ..... *C. peregrina*

2. Utricles long-rostrate utricle, stigmas two ..... 3.
2* Utricles erostrate utricle, stigmas three..... *C. acocksii*

3. Upper part of culm rounded, utricles glabrous or with sparse scabrid hairs ..... *C. monostachya*
3* Upper part of culm triangular, utricles at the edges terminally below the rostrellum with several scabrid hairs ..... 4. *C. runssoroensis*

4. Scales without hyaline margins, dark blackish-brown ..... *C. runssoroensis* var. *runssoroensis*
4* Scales with hyaline margins, dark brown ..... *C. runssoroensis* var. *aberdarensis*

***Carex acocksii* C.Archer**

S. African J. Bot. 63(6): 342 (1997). Type: South Africa, Northern Cape, Calvinia Distr., in vicinity of FM tower on top of Hantamsberg, Van Rhynshoek farm, 1580 m, 10. March 1987, *C. Reid* 1337 (holo. PRE; iso. BM, MO, NBG, P, S, TCD).

Habitat: Wet grassland

Distribution: South Africa, only known from type location at the top of the Hantamsberg

Notes: *C. acocksii* is similar to *C. monostachya* and *C. runssoroensis* but easily distinguished by the three (as opposed to two) stigmas and much larger, papery-transparent scales.

***Carex monostachya* A.Rich.**

Tent. Fl. Abyss. II: 512 (1851). *Uncinia digyna* Hochst. ex. Steud., Syn. Pl. Glumac. 2: 244 (1855) nom. illeg. Type: Ethiopia, GD, Simien, Mt Selki, at and above the limit of trees and shrubs, *W. Schimper* 687 (holo. P; iso. BM, BR, K, M, P, S, UPS).

C. triquetrifolia Boeckeler, Bot. Jahrb. Syst. 7: 279 (1886). *C. monostachya* A. Rich. var. *triquetrifolia* (Boeckeler) Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 74 (1909). Type: Tanzania, Mt. Kilimanjaro, *H.B. Johnston* 120 (holo.? K).
C. parasitica Kunze, Schkuhr, Beschr. Riedgräs., Suppl.: 83 (1842), nom. nud.

Habitat: Tussock forming on moist ground in grassland, swamps and along the edges of streams and lakes, occurring mainly in the alpine belt sometimes also ericaceous zone, (2400-) 2700-4500 m

Distribution: Ethiopia, Kenya, Tanzania, Eastern Uganda (Mt. Elgon)

Note: *C. monostachya* has been reported to form hybrid swarms with *C. runssoroensis* (Hedberg 1957) and can be difficult to distinguish as characters can be intermediate between these two species. In general *C. monostachya* has a distinct triangular stem (at least just below the inflorescence) and long, flat leaves, as opposed to a terete stem and short or absent leaves.

***Carex peregrina* Link.**

Hort. Berol. 1: 334 (1827). Type: Canary Islands (iso. M).

Habitat: Open grassland at mid altitudes

Distribution: Canary Islands, East Africa (Ethiopia, Kenya, Uganda and Northern Tanzania)

Notes: The disjunct distribution of *C. peregrina* over this large area from East Africa to the Canaries is also observed in other species (Andrus et al. 2004). The species is easily recognised by the presence of only a few (female 3-6(-8) and 3-6 male) flowers per spikelet and the thin, 1-3 mm wide, leaves. It is very similar in appearance to *S. filiforme* Kük.

***Carex runssoroensis* K.Schum.**

Engl. Pflanzenw. Ost Afr. C: 129 (1895). *Uncinia runssoroensis* (K.Schum.) Chiov. L. A. Savoia, II Ruwenzori, Relaz. Scient.: 466 (1909). Type: Uganda, Ruwenzori, rocky and mossy ground 3800 m, *Stuhlmann* 2454 (holo. B†; iso. K).

Note: See also comments under *C. monostachya,* which is the sister species of the more westerly distributed *C. runssoroensis. C. runssoroensis* is distinct by the terete (round) culm below the spike.

var. *runssoroensis*

Habitat: On flat, moist ground with poor drainage, usually as dominant species, 2750 – 4300 m.

Distribution: Uganda, Kenya, DR Congo, Rwanda

Notes: The variation *runssoroensis* is restricted to Uganda, Rwanda, Eastern DR Congo and Mt. Elgon in Kenya. Var. *runssoroensis* differs by its thicker culms and brown to blackish margins of the pistillate scales as opposed to thinner culms and the hyaline margin of its pistillate scales in *var. aberdarensis.* Var. *runssoroensis* can form large tussocks of more than one meter in diameter and 1.5 m in highest.

var. *aberdarensis* Kük.

Notizbl. Bot. Gart. Berl. 9: 311 (1925). Type: Kenya, Aberdares, Sattima, alpine region 4000 m, 21 March 1922, *Rob.E.Fries & Th.C.E.Fries* 2500 (K, UPS).

Habitat: On moist ground in the alpine region.

Distribution: Uganda, Kenya (Mt. Elgon, Cherangani Hills and more rare in Aberdare Mts. and Mt. Kenya)

Notes: Opinions differ as to whether varieties should be recognised within *C. runssoroensis*. Hains and Lye (1983) were against, whereas Hedberg (1957) and Verdcourt (pers. com.) were for recognising *var. aberdarensis*. Hedberg (1957) believed that it might represent a hybrid between *C. monostachya* and *C. runssoroensis*. Var. *aberdarensis* is more common in central and eastern Kenya than var. *runssoroensis*. According to Verdcourt (pers. com.) var. *aberdarensis* might prove to have what he describes as a creeping rhizome.

SUBGENUS *VIGNEA* (P.Beauv.) Nees

The subgenus Vignea is well supported as a monophyletic group in molecular phylogenetic analyses (Roalson 2001; Ford 2006). It is easily recognised by the branched terminal panicle and the lack of a prophyll. There are only relatively few Vignea species in Tropical and Southern Africa and none in Madagascar. Although Léveillé assigned erroneously *C. lebrunei* H.Lév. (sometimes also spelled *C. lebrunii*) to subgenus *Vignea*. The species was sunk by Chermezon into *C. renauldi* H.Lév., which belongs to subgenus *Carex*.

1. Inflorescence 1-20 cm long, spikelets 1 to numerous, in more or less close proximity, densely or loosely fruiting, ovoid, obovoid or elliptical ..... 2.
1* Inflorescence 2-3 cm long, spikelets 3-7, in close proximity, densely fruiting, ovoid or elliptical (introduced to Southern Africa) ..... *C. leporina*

2. Plants 10-20(-50) cm tall, leaves 1-3 mm wide; inflorescence 1-2 cm long, lower inflorescence bract scale like (North-eastern and Southern Africa) ..... 3.
2*. Plants >50 cm tall (rarely <50 cm tall); inflorescence >2 cm long, lower inflorescence bract scale like or leaf like (when plants <50 cm tall) ..... 4.

3. Pistillate scales with a broad (>0.5 mm wide) hyaline margin (Southern Africa) ..... *C. consanguinea*
3* Pistillate scales with an indistinct or narrow (0-0.5 mm wide) hyaline margin (Eritrea and Ethiopia) ..... C. *divisa*

4. Plants (60-)100-200 cm tall, stout; leaves (5-)8-15 mm wide; inflorescence 5-12 cm long and 1-2.5 cm wide, utricles (3.5-)4-5 mm long ..... 5.
4* Plants 20-100(-150), average or lean; leaves 3-8 mm wide, inflorescence 1-5(-8)cm long and 0.5-1.5 cm wide, utricles 3-5 mm long ..... 6.

5. Roots brown (never red); inflorescence often lax, utricles with 7-9 distinct veins on the convex side and 3-5 veins on the concave side (Eastern Africa south to Zimbabwe) ..... *C. lycurus*
5* Roots often red or brown; inflorescence dense, utricles with 3 veins on the convex side and 2 veins on the concave side (Ethiopia, possibly Kenya) ..... *C. koestlinii*
6. Roots brown (never red); utricles more or less scabrid, with 0-9 distinct or indistinct veins on the convex side and 0-5 veins on the concave side ..... 7.
6* Roots reddish; utricles never scabrid, with 7-9 distinct veins on the convex side and 2-3 veins on the concave side (North-eastern, Eastern Africa) ..... *C. erythrorrhiza*

7. Utricles more or less gradually narrowing towards the apex, rostrellum 1-1.5 mm long, sparsely to densely covered in scabrid hairs along the margins ..... 8.
7* Utricles gradually narrowing towards the apex, with a short (0.5-0.8 mm long), indistinct rostrellum, few fine hairs along the margins (Southern Africa) ..... *C. glomerabilis*

8. Leaves 4-8 mm wide; utricles with 0-3 veins on the convex side and no distinct veins on the concave side, the base never filled with corky material; achenes flattened with a rostrellum 0.5-1 mm long (North-eastern, Eastern and West Africa) ..... *C. conferta*
8* Leaves 2-5 mm wide; utricles with 5-8 veins on the convex side and 0-3 veins on the concave side, the base often filled with corky material; achenes trigonous with a rostrellum 1-2 mm long (North-eastern and Eastern Africa) ..... C. *leptosaccus*

***Carex conferta* Hochst. ex A. Rich.**

Tent. Fl. Abyss. 2: 512 (1850). Type: Ethiopia, Simien, near river in Enschedcap, 31. July 1839, *W. Schimper* 576 (holo. P; iso. BM, M, S, ST, K, UPS, Z).

C. conferta Hochst. ex A. Rich. var. *kilimandscharoana* Kük., nomen nudum (?) on material *H.J. Schlieben* 4818, 21. Feb. 1934, Tanzania, south-east of Mt. Kilimanjaro (Z) and *G. Volkens* 1544 (Z).

Habitat: On moist ground along streams, in swamps, occurring mainly in the upper part of the mountain forest belt and the ericaceous belt, 2300-3600 m.

Distribution: Ethiopia, Kenya, Northern Tanzania, Uganda, DR Congo, Rwanda, Cameroon

Note: Haines and Lye report that *C. conferta* has shorter utricles with less scabrid margins than *C. leptosaccus* and *C. lycurus*, however these differences do not appear to be consistent, and for these reasons Verdcourt does not consider these two species to be distinct. However, *C. conferta* differs from *C. leptosaccus* by having three veins on the convex side of the utricles (versus 5-8 in *C. leptosaccus*) and no (or indistinct) veins on the concave side (3 indistinct or distinct veins in *C. leptosaccus)*, and by the flattened achene with a short rostrellum 0.2-0.5 mm, as opposed to a trigonous achene with a 1-2 mm long rostrellum in *C. leptosaccus*. Following this distinction, most of the material currently identified as *C. leptosaccus* in fact represents *C. conferta*.

An additional varieties was annotated by Kükenthal on *Schlieben* 4818 and *Volkens* 1544 (var. *kilimandscharoana*). It differs from other material *of C. conferta* in that are no veins present (vs. 2-3 indistinct veins in *C. conferta*), the utricles are 4-5 mm long (vs. 3.5-4 mm) and the achenes 2.5 x 1 mm, obovoid and inflated (vs. 2 x 0.5 mm, ovoid and flat).

***Carex consanguinea* Kunth**

Enum. Pl. 2: 374 (1837). Type: South Africa, Western Cape Province, Little Namaqualand, between Pedros Kloof & Lily Fontein, 03. Nov. 1830, J.F. Drège 2450 (syn. BM, K, P,S, TCD).

Habitat: grassland (few locations with adequate records present)

Distribution: South Africa (Western Cape Province)

Notes: *C. consanguinea* has by some authors been regarded as a synonym of *C. divisa* Huds. Clarke (1902b) stated that in the South African form of *C. divisa* (= *C. consanguinea*) the angles of the stem are denssely scabrous, and the anthers have a long linear white crest; in the typical European *C. divisa* Huds, the angles of the stem are sparsely scabrous or smooth and the anthers are muticous or scarcely spiculate. It appears that the African *C. consanguinea* can also be separated from *C. divisa* by the hyaline wings of the inflorescence bracts. A more detailed analysis is needed to confirm this difference, especially since *C. divisa* has been reported as invasive from other region, for example Australia.

It should also be investigated whether *C. consanguinea* is distinct from *C. glomerabilis*, since the type collected by Drège resembles *C. glomerabilis.* However, most material of *C. consanguinea* seems to have a lower inflorescence bract which is scale like, 3-5 mm long, with hyaline margins, whereas the lower inflorescence bract of *C. glomerabilis* is leaf like and often very long, 8-15 mm long; without hyaline margins. Clarke (1902b) reports that the only differences between *C. divisa* and *C. glomerabilis* are that *C. divisa* is smaller with a smaller inflorescence and not bright-chestnut with green-margined utricles.

There is also a slight resemblance of *C. consanguinea* with *S. kunthinanum* Kük. and the absence of the rachilla should be confirmed while identifying material.

***Carex divisa* Huds.**

Fl. Angl.: 348 (1762). Type: England, *Newton* s.n. & *Sherard* s.n., England (OXF).

C. erythrorrhiza Boeckeler var. *curva* Chiov. (protolog not found). Type: Eritrea, Asmara, Mai-Belà, 05. May 1902, *Pappi* 5082 (Fl).

Habitat: Grassland (insufficiently known)

Distribution: Eritrea, N. Africa, Mediterranean, western & southern Europe, temperate Asia, introduced elsewhere

Notes: The name *C. divisa* has also been applied to material from South Africa by Kunth (see under *C. consanguinea*). *C. divisa* is a very variable species and the status of the material from Eritrea needs more careful investigation.

***Carex erythrorrhiza* Boeckeler**

Linnaea 39: 103 (1875) Type: Ethiopia, Simien Mts., near Debra Eski, 1853, *W. Schimper* 170 (syn. K); Ethiopia, Begemeder, Mt. Guna, thickets 3500 m, 10. Dec. 1863, *W. Schimper* 1556 (syn. K, M).

C. koestlini var. ß *minor* Boott, *Carex* ii. 76, t. 206, t. 207 (1860). Type: not indicated

Habitat: Grassland along streams, sometimes in wet places in the shade 2400-3500 m

Distribution: Ethiopia, Kenya

Notes: *C. erythrorrhiza* can best be distinguished from *C. leptosaccus* on the basis of the lack of scabrid hairs on the utricles (versus few to many hairs on the utricles towards the base of the rostrellum in *C. leptosaccus)* and the 7-9 veins in the convex side of the utricles (vs. 3-5 in *C. leptosaccus*). The diagnostic character used by Verdcourt: the colour of the roots; is not consistent within these species, thus some collections assigned to *C. erythrorrhiza* on this basis are in fact *C. leptosaccus*

C. erythrorrhiza can form big tussocks which can grow up to 1.5 m high and 30 cm in diameter. However, this growth-form seems to be restricted to the Cherangani Hills in Kenya as it has not been reported of Ethiopia (Verdcourt, pers. com.).

***Carex glomerabilis* Krecz.**

Not. Syst. Herb. Inst. Bot. Acad. Sc. URSS, 7: 34 (1937) nom. nov. pro *C. glomerata* Thunb. Prod. Pl. Cap. 14 (1794) 14., nom illeg. non Gmelin (1791) and Gilib (1792). Type: South Africa, Cape, without precise locality 1794, *C.P. Thunberg* 14 (holo. UPS).

C. schlechteri Nelmes, Bull. Misc. Inform. Kew: 269 (1940). Type: South Africa, Eastern Cape Province, Transkei, Bashee, 1600 m, 06 Jan. 1895R. *Schlechter* 6286 (holo. K; iso. BM, GRA, PRE).
C. leribensis Nelmes, Bull. Misc. Inform. Kew: 269 (1940) Southern Africa, Basutoland, Leribe Plateau, 1500 – 1800 m, *A. Dieterlen* 758 (holo. K; iso. BM, K, NH,P, PRE).

Habitat: In damp, grassland, or swamp margins. Occasionally in permanent water on fringes of *Typha* reed-beds.

Distribution: South Africa and Lesotho

Notes: Specimens of *C. glomerabilis* are often identified as *C. vulpina* L. or *C. otrubae* Pod. Nelmes (1940a) recognised three species in Southern Africa: C. *glomerabilis*, *C. leribensis* and *C. schlechteri*, in addition to the other South African *Vignea* species, *C. consanguinea*. He stated that *C. leribensis* is distinct from *C. glomerabilis* by the thinner leaves and smaller inflorescence and different base of the rostrellum and that *C. schlechteri* differs from *C. glomerabilis* by the wider leaves, the larger inflorescence and the more distinct nerves on the utricle. However, this distinction was not maintained and the species were again sunk into C. *glomerabilis* by Gordon-Gray (1995). The material of C. *glomerabilis* is however very variable and might yet consist of two species, one growing on margins of marshes and streams and another growing in grassland especially in the Drakensberg above 1300 m.

***Carex koestlinii* Hochst. ex Steud.**

Syn. Pl. Glumac. 2: 193 (1855). Type: Ethiopia, Simien Mts., Mt. Bachit, above Demerki 3600 m, 14. Aug. 1838, *W. Schimper* 1244 (syn. BR, K, M); Ethiopia, Simien Mts., *W. Schimper* 1539 (syn. M).

C. erythrorrhiza Steud., Syn. Pl. Glumac. 2: 194 (1855), nom. inval. without type.
C. erythrorrhiza Boeckeler *var. scabrida* Kük., Notizbl. Bot. Gart. Berl. 9: 313 (1925). (partially *C. leptosaccus*). Syntypes: Kenya, Mt. Kenya, moist places in forest 2350 m, 3. Jan. 1922, *Rob.E. & Th.C.E.Fries* 677 (syn. K, UPS). Kenya, Mt. Kenya, west, lower bamboo zone, along stream, 27. Jan. 1922, *Rob.E. & Th.C.E.Fries* 1212 (syn. UPS). Kenya, Aberdare Mts., Sattima, *Hagenia* region in swamp, 3300 m, 21. March 1922, *Rob.E. & Th.C.E.Fries* 2439 (syn. UPS).

Habitat: along streams

Distribution: Ethiopia, possibly also Kenya

Note: The rachillae of *C. koestlinii* are thin and flattened. Schuhmann in Engler (1892) sunl *C. koestlinii* in *C. steudneri* (which is a member of the subgenus *Indocarex*). This may be because the syntype (*W. Schimper* 1539 in M) represents *C. steudneri*, rather than *C. koestlinii*. Kükenthal (1902) accepted *C. koestlinii* as a separate species but sunk *C. leptosaccus* in it.

C. koestlinii resembles a bigger version of *C. leptosaccus* but with red roots and broader leaves. It is very similar to *C. lycurus*, however the inflorescence bracts and bracteoles are leaf like (vs. bract like in *C. lycurus*), and the utricles have 3 distinct veins on the convex side (vs. 7-9 in *C. lycurus*). *C. koestlinii* differs from *C. erythrorrhiza* (which also has red roots) in its much broader, 5-8 mm wide, leaves and scabrid utricles (vs. 1-3 mm wide leaves and glabrous utricle in *C. erythrorrhiza*). It differs from *C. conferta* in the reddish roots, slightly broader leaves (2-5(-8) mm wide in *C. conferta*) and utricles with a longer, 1-1.5 mm long, rostrellum (1-1.3 mm long rostrellum in *C. conferta*).

***Carex leporina* L.**

Sp. Pl.: 973 (1753)

Note: *C. leporina* was probably introduced in South Africa from Europe. It is easy to recognise because of the dense ovoid spikelets which are more or less crowded at the tip. It is somewhat similar to *C. balfourii* Kük., from La Réunion.

***Carex leptosaccus* C.B.Clarke**

Fl. Trop. Afr. 8: 516 (1902). *C. conferta* Hochst. ex A. Rich. var. *leptosaccus* (C.B.Clarke) Kük., Notizbl. Bot. Gart. Berl. 9: 312 (1925) and sensu Lye in Nordic J. Bot. 3: 244 (1983). Type: Tanzania, Mt. Kilimanjaro, Sept. 1894, *Thompson s.n.* (holo. K.)

C. erythrorrhiza Boeckeler *var. scabrida* Kük., Notizbl. Bot. Gart. Berl. 9: 313 (1925). (partially *C. koestlinii*). Syntypes: Kenya, Mt. Kenya, moist places in forest 2350 m, 3. Jan. 1922, *Rob.E. & Th.C.E.Fries* 677 (syn. K, UPS). Kenya, Mt. Kenya, west, lower bamboo zone, along stream, 27. Jan. 1922, *Rob.E. & Th.C.E.Fries* 1212 (syn. UPS). Kenya, Aberdare Mts., Sattima, *Hagenia* region in swamp, 3300 m, 21. March 1922, *Rob.E. & Th.C.E.Fries* 2439 (syn. UPS).

Habitat: along streams and wet places between stones

Distribution: Ethiopia, Kenya, Uganda, Northern Tanzania, DR Congo, probably also Rwanda

Note: Clarke assigned the name *C. leptosaccus* a second time in the same year for material outside Africa (Bot. J. Linn. Soc. 35 (1902): 404, printed on 30. July 1903). The description of the African material was published first, and thus the later application of the name is invalid.

C. leptosaccus bears a resemblance to *C. conferta*, *C. koestlinii* and *C. lycurus.* Kükenthal (1909: 411) listed *C. leptosaccus* as a synonym of *C. koestlinii*; Haines and Lye (1983: 244) and Verdcourt (pers. comm.) treat material of *C. leptosaccus* as a variety of *C. conferta.* Differences between these taxa are however consistent and *C. leptosaccus* warrants recognition as a distinct species. For differences to *C. conferta* see the notes under that species. *C. leptosaccus* has leaves 2-5 mm wide (vs. 5-12 mm in *C. lycurus* and 5-8 in *C. koestlinii*) and utricles with 0-3 veins on the concave side (vs. 4-5 in *C. lycurus*). In contrast to *C. koestlinii*, the rachilla of *C. leptosaccus* is inconspicuous (as opposed to long and flattened) and the roots are not red.

***Carex lycurus* K.Schum. ex Engl.**

Abhandl. Preuss. Akad. Wiss.: 58 (1894); et in Engl. Pflanzenw. Ost Afr. C: 129 (1895). *C. conferta* Hochst. ex A. Rich. var. *lycurus* (K.Schum.) Lye Nordic J. Bot. 3(2): 244 (1983). Type: Tanzania, Usambara, Heboma, *C. Holst* 2554 (holo. B†; hololecto. K; isolecto. M, Z), lectotype assigned by Haines and Lye (1983). Syntype: Usambara, Kwa Mshuza, meadows, Tanzania Aug. 1893, *C. Holst* 8971 (holosyn. P; isosyn. M, K, Z).

C. robinsonii Podl. Mitt. Bot. Staatssamml. München 4: 122 (1961). Type: Zambia, Nyika Plateau, shady streamside, 2. Jan. 1959, E.A. Robinson 3000 (holo. M).

Habitat: Open upland grassland, in moist places, along streams

Distribution: Tanzania, Kenya, Malawi, Zambia, Zimbabwe

Note: *C. lycurus* is similar to *C. conferta* and *C. leptosaccus* (see also notes under the species). It is a stout, broad leaved species (leaves 5-12 mm wide) with (5-)7-9 distinct veins on the convex side of the utricles and 3-5 veins on the concave side, achene with long rostrellum 1-2 mm. Haines and Lye (1983) state that *C. lycurus* only occurs in Tanzania and Kenya (west of the Aberdares). However, the species is also present on Mt. Elgon.

SUBGENUS *CAREX*

Subgenus *Carex* is the largest in *Carex*. Species delimitation in Africa varies widely between authors. The most comprehensive account of East Africa has been published by Haines and Lye (1983), which has been revised by Verdcourt (pers. comm.). The species in Madagascar have been fairly well studied by Chermezon (1937). For the key presented here we have investigated vegetative characters more intensely than reported by Clarke (1902a), Haines and Lye (1983) or Verdcourt (pers. comm.) because they are independent of the maturity of the utricle. Other important diagnostic characters in this group are the distribution of male and female "florets" (i.e. spikelets consisting of the reduced flower, the utricle and the scale), the size and shape of the utricle. The indumentum and exact number of veins is only used exceptionally here, as they seem to vary within species. It is in many cases difficult to determine young material and unfortunately not all the type material is fully mature. This has probably contributed to taxonomic instability in this group. The lateral branching of spikelets is probably not suitable for species delimitation.

1. Spikelets lax (utricles sparse, overlapping by less than half of their length), utricles 7-12 mm long, very gradually tapering (Madagascar and Eastern Africa south to Malawi) ..... 2.
1* Spikelets dense (utricles overlapping by at least half of their length), utricles 2-8 mm long, gradually tapering or abruptly narrowed into rostrellum or no rostrellum present ..... 4.

2. Flowers 4 or more per spikelet, spikelets branched (Eastern Africa south to Malawi) ..... 3.
2* Flowers 2-4 per spikelet, spikelets unbranched (Madagascar) ..... *C. renauldi*

3. Flowers few (2-4) per spikelet, unbranched, spikelets sparse (western part of East Africa) ..... *C. biegensis*
3* Flowers > 2-4 per spikelet, unbranched, spikelets dense (Eastern Africa south to Malawi) ..... *C. johnstonii*

4. Utricles without a rostrellum, or, if with a short rostrellum, then without teeth (the orrect interpretation of this character requires careful investigation on both sides of the utricles as one side can show dentations that resemble teeth when seen from one side), styles 2 or 3 ..... 5.
4* Utricles with a well developed rostrellum, or at least with clearly visible teeth, styles 3 ..... 14.

5. Utricles flattened, styles 2 ..... 6.
5* Utricles not flattened, styles 3 (rarely some florets with 2) ..... 9.

6. Utricles with several distinct veins (Northern East Africa, Madagascar) ..... 7.
6* Utricles without distinct veins ..... 8.

7. Rostrellum present, spikelets 1-5 cm long (Northern East Africa, Madagascar) ..... *C. brunnea*
7* Rostrellum absent, spikelets 6-18 cm long (Madagascar) ..... *C. baronii*

8. Utricles covered with dense distinct papillae, awn long but

never longer than the utricle (Madagascar, Southern Tanzania) ..... 9.
8* Utricles not densely papillate, if papillate then papillae short, awn of pistillate cales much longer than the utricles (Southern Africa, Zimbabwe and possibly Malawi) ..... *C. austro-africana*

9. Pistillate scales 1.8-2.5 mm long, broadly lobed (Madagascar) ..... *C. madagascariensis*
9* Pistillate scales 3-4 mm long, narrowly lobed (Southern Tanzania) ..... *C. papilossisima*

10* Plants 10-180 cm tall, leaves 3-4 mm wide, female spikelets, upright or dropping utricles smooth and with a few papillae (Madagascar, Southern Africa) ..... 11.
10. Plants 10-30 cm tall, leaves 3-4 mm wide, all spikelets upright, utricles glabrous (Southern Africa) ..... *C. burchelliana*

11. Utricles smooth or with a few papillae, male spikelets 1-2, terminal; female spikelets 1-8, drooping (Madagascar, Southern Africa) ..... 12.
11* Utricles covered in dense papillae, male spikelets 2-3, terminal; female spikelets 3-4, upright (Southern Africa) ..... *C. acutiformis*

12. Utricles 3-4 mm long, pistillate scales 4-9 mm long (continental Africa) ..... 13.
12* Utricles 3 mm long, pistillate scales 3 mm long (Madagascar) ..... *C. penduliformis*

13. Utricles 3-4 mm long (North-eastern and Eastern Africa) ..... *C. bequaertii*
13* Utricles 2-3 mm long (Southern Africa) ..... *C. mossii*

14. Spikelets crowded, upright, sessile to short pedunculate, utricles dense, often inflated, 3-6 mm long ..... 15.
14* Spikes usually not all crowded, often drooping, pedunculate (at least the basal ones),utricles dense or loose, rarely inflated, 3-6 mm long if spikelets are not crowded, if spikelets crowded, then utricles >6 mm long ..... 21.

15. Spikelets never >3 cm long, all crowded towards the tip, rarely one spikelet more distant (Southern Africa) ..... 16.
15* At least some spikelets >3 cm long, not all crowded towards the tip but at least some spikelets more distant ..... 17.

16. Plants 5-10 (-15) cm tall, utricles 4-5 mm long, rostrellum very gradually tapering, 1.5-2 mm long (Upper Drakensberg Plateau) ..... *C. monotropa*
16* Plants often >20 cm tall, utricles 4-5 mm long, rostrellum not gradually tapering, 1-1.2 mm long (Western Cape) ..... *C. ecklonii*

17. Pistillate scale awns 1-3 (-4) mm long, glabrous or scabrid ..... 18.
17* Pistillate scales awns 0.5-1 mm long, not scabrid (Southern Africa) ..... *C. subinflata*

18. Spikelets 2-3(-4) mm long, utricles inflated at maturity, with or without distinct, robust, 0.5-0.8 mm long teeth (South Africa) ..... 19.
18* Spikelets 5-8 mm long, utricles not inflated at maturity, with distinct, fine, 1 mm long teeth (South Africa) ..... *C. drakensbergensis*

19* Leaves 3-7 mm wide; spikelets 3-10 cm long and 0.5-1 cm wide, awn of the pistillate 1.5-2 mm long, more or less scabrid (continental Africa) ..... 20.
19. Leaves 2-6 mm wide; spikelets 3-6 cm long and 0.6-0.8 mm wide, awn of the pistillate scales 1.5-2 mm long, scabrid (Madagascar) ..... *C. sphaerogyna*

20. Pistillate scales 4-5 mm long, green or brown, sometimes scabrid, utricles glabrous (Eastern Africa and Southern Africa) ..... *C. sp. A* (= *C. cognata*)
20* Pistillate scales 5.5-7 mm long, usually dark brown and densely

scabrid, utricles covered in fine hairs, especially in the upper part
(Eastern Africa) ..... *C. phragmitoides*

21. Spikelets mostly or all short pedunculate, some erect
(avoid too young material), spikelets always arising individually ..... 22.
21* Spikelets mostly long pedunculate and pendulous (avoid too young
material) or al least not more than 0.8 mm wide, spikelets arising
individually or in pairs, sometimes even 3-4 spikelet per bract present ..... 26.

22. Leaves coriaceous and erect, pistillate and staminoid scales dark
brown to black, few utricles greenish or with brown dots ..... 23.
22* Leaves not coriaceous, pistillate and staminoid scales green,
brown or red, utricles green, brown or reddish (Southern Africa) ..... 24.

23. Utricles 2.5-3 mm long, densely papillose (South Africa) ..... *C. acutiformis*
23* Utricles 5-6 mm long, glabrous, without papillae (Eastern Africa) ..... *C. simensis*

24. Utricles 4-6 mm long, rostrellum 0.5-1 mm long, teeth present but
not prominent, pistillate scales 3-6 x 2-2.5 mm ..... 25.
24* Utricles 6-7.5 mm, rostrellum 1.5 mm long with prominent teeth,
pistillate scales 6-7 x 3 mm (Western Cape Province) ..... *C. clavata*

25. Spiklets 5-8 mm wide, utricles 5-6 x 2 mm, pistillate scales
3-5 mm long (Southern Africa) ..... *C. aethiopica*
25* Spiklets 8-1.0 mm wide, utricles 5.5-6.5 mm long, pistillate
(scales 5-6 mm long Eastern part of Southern Africa) ..... *C. subinflata*

26. Utricles 3-8 mm long, with or without distinct beak, without
thin teeth, c. (Madagascar, West, Northeast and East Africa, south
to Malawi) ..... 27.
26* Utricles 4.5-5 mm long, with distinct beak and c. 1mm long, thin
teeth, (sometimes breaking of while handling) (Southern Africa) ..... *C. drakensbergensis*

27. Plants 30-200 cm tall; utricles at least 4 mm long ..... 29.
27* Plants 30-70 cm tall; utricles 3-3.5 mm (North-eastern Africa and
Madagascar) ..... 28. *C. brunnea*

28. Pistillate scales 2.5-3 mm long (Madagascar) ..... *C. brunnea* var. *masoalensis*
28* Pistillate scales 3-4 mm long (North-eastern Africa) ..... *C. brunnea* subsp. *occidentalis*

29. Utricles at least 6 mm long ..... 30.
29* Utricles 4-6 mm long ..... 31.

30. Pistillate scales dark or light brown, utricles green, brown,
blackish or reddish (Madagascar) ..... *C. humberti*
30* Pistillate scales dark, utricles contrasting green (Ethiopia and
Eastern Africa) ..... *C. simensis*

31. Leaves not coriaceous, base yellow, red or brown; spikelets not
appearing pyramidal ..... 32.
31* Leaves coriaceous, base yellow; spikelets with dense utricles at
the base, less dense towards the apex, giving them a distinct pyramidal
look (Eastern Africa south to Zimbabwe and West Africa) ..... *C. cuprea*

32. Spikelets 2-5, arising together ..... 33.
32* Spikelets usually single, rarely in pairs ..... 36.

33. Spikelets usually more than 10 times as long as wide ..... 34.
33* Spikelets usually no more than 6 times as long as wide ..... 35.

34. Utricles 5-6 mm long (Eastern Africa) ..... *C. vallis-rosetto*
34* Utricles 4 mm long (Madagascar) ..... *C. boryana*

35. Spikelets 4-8 mm wide, utricles 4-5 mm long (Western Africa) ..... *C. mannii*
35* Spikelets 8-10 mm wide, utricles 5-6 mm long (North-eastern and Eastern Africa) ..... *C. thomasii*

36. Leaf base dark red, rarely yellow; spikelets usually more than 10 times as long as wide, scales brown to dark brown, utricles green to light brown ..... 37.
36* Leaf base brown or yellow; spikelets usually no more than 6 times as long as wide, scales and utricles light to dark brown ..... *C. petitiana*

37. Utricles with more than two distinct or fine nerves (North-eastern and Eastern Africa, West Africa) ..... 38.
37* Utricles with two distinct nerves (South Africa) ..... *C.* cf. *sylvatica*

38. Leaf base brown, yellow or orange, never red; utricles 4.5–6 mm long..... 39.
38* Leaf base dark red or at least distinct reddish; utricles 3.5-4.5 mm long..... ..... C. *ninagongensis*

39. Utricles 5-6 mm long (North-eastern and Eastern Africa). ..... *C. longipedunculata*
39* Utricles 4.5-5 mm long (West Africa) ..... *C. preussii*

***Carex acutiformis* Ehrh.**

Beitr. zur Naturk. IV: 43 (1789). Type: Germany: in paludosis Brunsvico-Luneburgicis, 100-2200 m, s.c., s.n. (type locality not cited)

Habitat: Usually in water on the margins of ponds, along streams and rivers.

Distribution: Widely distributed in warm and temperate regions in Europe, Asia, North America and Northern & Southern Africa

Notes: *C. acutiformis* is probably not present in north-eastern and eastern Africa despite being mentioned for these areas due to misidentifications. *C. acutiformis* Ehrh. is considered to be introduced in Africa. However, the South African material differs from the European and might represent a distinct species. Clarke (1897/98) stated that the African material has pistillate scales with scabrid awns while the European material is glabrous; the African material has a very short rostrellum (0-0.2 mm long) and a achene wider than long, whereas the European material has a rostrellum 0.2-0.5(-0.7) mm long and the achene is 2/3 as wide as long. The African material also differs by the dense papillose utricles (as opposed to glabrous to scarcely papillose in European material). However, some African material with smaller utricles (2.5-3 mm long) and smaller pistillate scales (2-2.5 mm long including a 0.5-1 mm long scabrid awn) has distinct teeth and a distinct, short, abruptly narrowing rostrellum (0.5 mm long). The status of this material and the relationship to the material from Europe needs further investigation.

***Carex aethiopica* Schkuhr**

Riedgr. t. Z. fig. 83: 107 (1801). *C. aethiopica* Boott, *Carex* 3: 110, t.344 (1862). Type: South Africa, *J.F. Drège* 550 and 743 (syn. K see notes).

C. iridifolia Kunth, Enum. Pl. 2: 492; (1837). *C. aethiopica* Schkuhr var. *iridifolia* (Kunth) C.B.Clarke, Consp. Fl. Afr.: 679 (1894). Type: South Africa , Ruigtevalei, 23. Sept. 1831, *J.F. Drège* 7398 (P).

Habitat: wet places in the full sun at forest margins or along streams in the shade

Distribution: Southern Africa

Note: There has been much confusion about the type material of *C. aethiopica:* Engler (1892: 152) cited *Schimper* 1180 and 1289 from Ethiopia as well as *Mann* 2099 from Cameroon and mentioned var. *stolonifera* Boeckeler l.c. 1550 citing Schimper 1863 and 1298.

Durand (1894: 679) assigned *C. aethiopica* var. *aethiopica* only to the material from Cameroon (Mann 2099) and divided the rest into *C. aethiopica* var. *iridifolia* from South Africa and *C. aethiopica* var. *stolonifera* (= *C. cuprea*) to material from Ethiopia.

Clarke (1898: 308) stated that the type is Thunberg in South Africa and not on La Réunion as originally cited by Schkuhr. But noted on material from Drège 550 and 743 that this might be the type material. Later he identified at least the material of Schimper 1298 as *C. simensis* C.B.Clarke (stated on the type material as Feb. 1899 which was changed by Nelmes in 1938 to *C. cuprea* (Kük.) Nelmes.). He also recognised *C. aethiopica* var. ß *latispica* which has been sunk in *C. clavata*.

Kükenthal (1909: 654) recognised *C. aethiopica* as confined to South Africa in which he brought *C. iridifolia* and *C. aethiopica* var. *iridifolia* into synonymy.

C. Archer annotated material from Drège in BM and K as Drège 7398 and therefore as isotype material of *C. iridifolia* even though the label says 550 & 743.

Differences to other African species: Utricles 5.5-6.5 mm long, female spikelets 7-9 mm wide, subsessile to short pedunculate, mostly erect. The material from the Eastern parts of South Africa seems to be larger in all parts (width and length of the spikelets, leaves, utricles etc.) the differences are gradual and are probably not enough to separate them as a distinct taxon.

***Carex austro-africana* (Kük.) Raymond**

Natur. Canad. 91: 126 (1964). *C. cernua* Boott var. *austro-africana* Kük., Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 354 (1909). Type: South Africa, Mooi River, Dec. 1890, *J.M. Wood* 1690 (holo. BM; iso. Z).

C. rhodesiaca Nelmes, Bull. Misc. Inform. Kew: 159 (1939). Type: Zimbabwe, Mwinilunga District, by Lunga, in muddy pockets of rocks, full of water, 27. Nov. 1937, *E.W.B.H. Milne-Redhead* 3422 (holo. K?; iso. B, BR, PRE).

Habitat: wet areas of vleis and streamlets, sometimes on hummocks, but often rooted in shallow slowly flowing water. Occasionally they fringe *Typha* reedbeds in deeper water

Distribution: Southern Africa, Zimbabwe and possibly Malawi

Notes: Closely related to *C. phacota* Spreng from Tropical and Subtropical Asia. Utricles green, yellow or white when fresh (see Figure 1) becoming brownish-green when dry. Nelmes states that *C. rhodesiaca* is close to *C. cernua* Boott distinct through terminal spikes being male and sometimes gynaecandrous, and its only striking and consisting difference from the species lies in much longer pistillate scales. However, he overlooked that Kükenthal (1909: 354) has described the same characters as differences between *C. cernua* var. *austro-africana* and var. *cernua* which was later raised to the status of species by Raymond.

***Carex baronii* Baker**

J. Linn. Soc., Bot. 21: 451 (1885). Type: Madagascar, *R. Baron* 2795 (syn. P, K).

Habitat: forest at stream edges, 700-1500 m

Distribution: Central and East Madagascar

Note: Very similar to *C. madagascariensis* and other members of the Section *Praelongae* Kük. from Africa (*C. austro-africana* from Southern Africa and *C. papilossisima* from Southern Tanzania) but distinct through the distinct veins on the utricle, as opposed to indistinct veins, in other members of the Section *Praelongae*.

***Carex bequaertii* DeWild.**

Pl. Bequaert. IV: 246 (1927). Type: DR Congo, Ruwenzori Mts., Lanuri Valley 3000 m, *Bequaert* 4677 (holo. BR; iso. K).

Carex bequaertii DeWild. var. *maxima* Lye, Nordic J. Bot. 3(2): 244 (1983). Type: Uganda, Karamoja district, Mt. Morungole, 2440 m, Apr 1960, *J. Wilson* 1012 (holo. EA; iso. K).
C. robusta Hochst. Pl. Abyss. (1850). Type: Ethiopia, *W. Schimper* 100 (type location not found).

Habitat: On moist ground along streams and lakes and in swamps, 2600-4000 m

Distribution: Ethiopia, Kenya, Tanzania, Uganda, DR Congo, Rwanda

Notes: Very closely related to *C. mossii* Nelmes from South Africa and *C. penduliformis* from Madagascar and difficult to distinguish. Similar also to *C. pendula* Huds. from Europe. Distinct from other African *Carex* species by the large size (leaves 12-15 mm wide, spikelets 4-22 cm long and 7-10 mm wide) and the utricles with a short rostrellum without teeth.

C. bequaertii var. *maxima* is only distinguished from var. *bequaertii* by its even larger size and broader spikelets (about 10 mm wide with 6-9 mm long pistillate scales, as opposed to 7-8(-10) mm wide spikelets with 4-6 mm long pistillate scales in var. *bequaertii*). *C. bequaertii* is very variable in size and var. *maxima* does not deserve a status as a distinct variation.

***Carex biegensis* Cherm.**

Bull. Soc. Bot. France 82: 343 (1935). Type: DR Congo, Kivu region, Mt. Biega, south of Kahuzi, 2400-2790 m, March 1929, *H. Humbert* 7679, 7679 bis (syn. P).

Habitat: in open places in the forest 2500-2800 m

Distribution: DR Congo, Uganda, Rwanda, Tanzania

Notes: Verdcourt mentions a dark coloured variation of *C. johnstonii* Boeckeler based on material of Luke et al. 6905. This material may belong to *C. biegensis* .

***Carex boryana* Schkuhr**

Beschr. Riedgräs. 2: 43 (1806). Type: La Réunion, J.B.G.M. *Bory de St-Vincent* s.n. (P).

C. boryana Schkuhr var. *simplicissima* Kük., Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 651 (1909) p.p. (see also *C. mannii* and *C. vallis-rosetto*). Syntypes: Fernando Po, Clarence Peak, *Mann* 661 (syn. K). Fernando Po, Clarence Peak, *Mann* 1478 (syn. K). Uganda, Rwenzori Mts., *Scott-Elliott* 7873 (syn. K) La Réunion, *Boivin* 997 (syn. P).
C. boryana var. *β minor* Boott ex Boeckeler, *Carex* 3: 111 (1862) et Linnaea 41: 285 (1877) (see also *C. mannii*). *C. boryana* var. *γ rigidifolia* Boeckeler, Linnaea 41: 285 (1877). Syntype: La Réunion, *Boivin*, 996 et 997 p.p. (syn. P)
C. giraudiana Steud., Syn. Pl. Glumac. 2: 209 (1855): La Réunion, 1847, *H. Giraudy* s.n. (P).

Habitat: wet places in forest understory

Distribution: Madagascar, La Réunion

Notes: See also C.B.Clarke (1885: 451). Records from West Africa or North-eastern Africa are misidentifications.

***Carex brunnea* Thunb.**

Fl. Japon 38: (1784). Type: Japan, *Thunberg* s.n., microfiche 21769 (holo. Herb. Thunberg-UPS)

Habitat: in shade or on wet grassland

Distribution: Asia (from India to Japan), Madagascar, Mascarenes, Arabian Peninsular

Notes: In Flora of Northeast India it is stated that *C. brunnea* as understood by Clarke and Kükenthal contained three distinct species, viz. *C. brunnea* Thunb. (from China, Japan and Indo-china) *C. hattoriana* Nakai (from Japan, Malaya and Australia) and *C. lenta* D. Don (from Himalayas, China and Japan). For Tropical Africa two subspecies or varieties of *C.*

brunnea in the strict sense have been described: Another variety, *C. brunnea* Thunb. var. *arabica* Hooper (1984), occurs in Yemen. It is not further discussed here.

subsp. *brunnea*

Habitat: in shade or on wet grassland

Distribution: Asia (from India to Japan)

subsp. *occidentalis* Lye

Bull. Mus. Nation. Hist. Nat., B, Adansonia, Ser. 4, 18 (3–4): 235 (1996). Type: Somalia, Sanaag Region, 11. Jan 1995, *Thulin et al.* 8982 (holo. UPS; iso. K).

Habitat: Rocky gully in shade

Distribution: Somalia and Ethiopia

Notes: Very similar to *C. brunnea* Thunb. var. *arabica* S.S.Hooper. from Yemen

var. *masoalensis* Cherm.

Cat. pl. Mad., Cyp.: 45 (1931) *C. masoalensis* Cherm., Bull. Soc. Bot. France 70: 414 (1923). Type: Madagascar, Masoala, *H. Perrier de la Bâthie* 2576 (P).

Habitat: Rocks near streams

Distribution: Northern Madagascar

Notes: Utricles, 3 mm long, slightly shorter than in *C. brunnea* Thunb. *var. brunnea,* including a long rostrellum.

***Carex burchelliana* Boeckeler**

Linnaea 41: 234 (1877). Type: South Africa, Cape Prov., Kalahari Region, Hay Div., at Griqua Town, 13. Dec. 1811, *W. J. Burchell* 1911 (lecto. K; isolecto. P), lectotype annotated by C. Archer.

C. flavecsens Burchell, South Africa, Griqualand West Herbert Division, Upper Campbell. Original coll. Trav. I 467, 18. Nov. 1811, *W. J. Burchell* 1831 (syn. K, P).

Habitat: marshes or standing water often with *Typha*

Distribution: South Africa, Western Cape Province

Notes: *C. burchelliana* is similar to *C. clavata* at first sight but it has utricles with very short, 0.2-0.5 mm long rostrellum and no teeth, the midribs of the pistillate scales end in short tips, opposed to *C. clavata* which has utricle with a 1.5 mm long rostrellum and with prominent teeth and the pistillate scale with a midrib which ends in an elongated tip. *C. ecklonii* which is also similar has much utricles which are abruptly narrowed into the 1mm long rostrellum.

***Carex clavata* Thunb.**

Prod. Pl. Cap.: 14 (1794). Type: Cape of Good Hope, *Thunberg* s.n. (holo. UPS; iso. S).

C. aethiopica Schkuhr var. *latispica* C.B.Clarke, Consp. Fl. Afr.: 679 (1894). Type: South Africa, Western Cape Province, Albany Division, Bothasberg, *P. MacOwan* 1013 (K, S).

C. ecklonii Nees var. α, Linnaea 10: 203 (1836). Type: South Africa, Western Cape Province, Uitenhage, Sea View near Cape Recife, close to Lévrew (Leeview), *C.F. Ecklon & C.L.P. Zeyher* 912 ().
C. extensa Good. var. *β ecklonii* (Nees) Kük. Synypes: South Africa, *Kemsley* 186 and Scottland, *Ch. Bailey* apud *Kneucker* 214 (Z)
C. lutensis Kunth, fide Fl. Cap. 7: 309 (1898) non Enum. Pl. 2 (1837): 487. *C. clavata* forma *lutensis* (Kunth) Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 737 (1909). Syntypes: South Africa, Western Cape Province, Groene Kloof, 26.11.1827, *J.F. Drège* 1563 (syn. K, P, S, BM, TCD). South Africa, Western Cape Province, Paarlberg, *J.F. Drège* 1583 (P).

Habitat: Permanently wet places, in full swamps, marshes and seasonally flooded places. Mostly ± at sea level and usually near the coast.

Distribution: Western Cape Province

Note: The type material of *C. clavata* in S is mounted on a sheet with a second collection from Hasselt, Kuki and Reinweardt s.n. (annotated as such by C. Archer). The collection by *Thunberg* s.n. is immature. However the name has been consistently used. Some of the type material mentioned by Kükenthal seems to belong to *C. ecklonii* and the two species need a more careful assessment. Although similar to *C. burchelliana* at first sight, *C. clavata* has prominent teeth and a shiny utricle and the female scale has a midrib which ends in an elongated tip, unlike *C. burchelliana* which possesses utricles with short beaks, without teeth, and female scales with midribs which end in short tips. *C. ecklonii* has much smaller utricles (4-5 mm compared to 6-7.5 mm long in *C. clavata*).

Carex cuprea (Kük.) Nelmes

Bull. Misc. Inform. Kew: 247 (1938) *C. longipedunculata* K.Schum. subsp. *cuprea* Kük. Notizbl. Bot. Gart. Berl. 9: 315 (1925). Syntypes: Kenya, Mt. Aberdares, Forrest Station, 2300 m, 1921-22, *Rob.E. & Th.C.E.Fries* 405 (holosyn. UPS; isosyn. K) and Kenya, near 'West Kenya Forest Station' Mt. Aberdare, 04 Jan. 1922, *Rob.E. & Th.C.E.Fries* 734 (holosyn. UPS; isosyn. K).

C. aethiopica Schkuhr var. *stolonifera* Boeckeler Linnaea 41: 286 (1877). *C. simensis* Hochst. ex. A.Rich. var. *stolonifera* (Boeckeler) Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 654 (1909). Syntype: Ethiopia, Begemder near Gafat, near Tabor, 22. Aug. 1863, *W. Schimper* 1298 (syn. K, M).
C. longipedunculata K.Schum. subsp. *cuprea* Kük. var. *atronnata* Kük. (or *atrennata*) protolog not found Type: Zimbabwe, near Inyanga, at the river Kuhera, 1800 m, 20. Nov. 1930, *Rob.E. & Th.C.E.Fries, T. Norlindh and H. Weimarck* 3094 (S).

Habitat: Wet places in forest or swamps

Distribution: Ethiopia, Kenya, Uganda, Northern and Southern Tanzania, Malawi, Zimbabwe, West Africa (Cameroon and Nigeria)

Notes: Haines and Lye (1983) and Verdcourt (pers. com.) do not recognise *C. cuprea* as a distinct species. However, it differs from other African *Carex* species by the prominent spikelets which have very dense utricles at the base and less dense female flowers towards the apex of each spikelets giving them a distinct pyramidal look. The leaf base is always yellow or orange and the leaves are 8-12 mm wide. See also comments on *C. petitiana* A. Rich.

Carex *drakensbergensis* C.B.Clarke

Fl. Cap. 7: 309 (1898) *C. cognata* Kunth var. *drakensbergensis* (C.B.Clarke) Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 699 (1909). Type: South Africa, East Griqualand, Near Kokstad, 18. Dec. 1889, J. *Medley-Wood ex W. Haygarth* 4201 (Isolecto. NH annotated on type by C. Archer).

Habitat: wet places often standing in water

Distribution: Southern Africa (Drakensberg)

Note: Other material originally mentioned Nelson 72, South Africa, Transvaal, Mooi River, near Potchenstroom; Buchanan 112, South Africa, Drakensberg, near Harrismith; Buchanan 136, April 1883, South Africa; Buchanan 137, April 1883, South Africa, Natal.(K); Galpin 6881, South Africa, Barkley East

There is some similarity between *C. drakensbergensis* and *C. sp. A.* (previously often misapplied as *C. cognata*, see discussion under *C. sp. A* and *C. ecklonii*). *C. drakensbergensis* differs from *C. sp. A.* by the bigger, 5-8 mm long, spikelets, which are more evenly spaces along the culm, the utricles, which are not inflated at maturity and the 1 mm long, fine teeth, as opposed to spikelets terminally clustered, utricle inflated at maturity with long, fine or broad, 0.5-1.5 mm long, teeth.

***Carex ecklonii* Nees**

Linnaea 10: 203 (1836). *C. ecklonii* Nees var. β Linnaea 10: 203 (1836). *C. extensa* Good. var. β *ecklonii* (Nees) Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 203 (1909).Type: South Africa, Western Cape Province, Zwellendam and George, *Mundt* 91 (S).

C. rehmanniana Boeckeler protologue not found Type: South Africa, Rehmann 1793 (Z).

C. clavata Thunb. var. *campylostachya* Nees, Linnaea 10: 204 (1836). Type: South Africa, Western Cape Province, Uitenhage, Sea View near Cape Recife, *C.F. Ecklon & C.L.P. Zeyher 121* (syn. PRE, S).

Habitat: meadows near the coast

Distribution: South Africa, Western Cape

Notes: Nees lists two variations in the original publication of *C. ecklonii*. Var. α or *latifolia* with wider leaves and longer utricles (Type: South Africa, Western Cape Province, Uitenhage, Sea View near Cape Recife, close to Lévrew (Leeview) *Ecklon and Zeyher* 82 or 912) and var. β or *angustifolia* (Type: South Africa Western Cape Province, Zwellendam and George, *Mundt* which is probably *Mundt* 91) with smaller leaves and longer utricles. *Mundt* 91 is also the type collection of *C. cognata* Kunth. (1837: 502) (see notes on *C. sp. A*).

Kükenthal (1909: 667, 697, 736) listed var. β under *C. cognata* Kunth, citing var. α as a synonym of *C. extensa* Good. var. β *ecklonii* (Nees) Kük. (Synypes: South Africa, *Kemsley* 186 and Scottland, *Ch. Bailey* apud *Kneucker* 214) while referreing to the type material of var. α (*Ecklon and Zeyher* in Nees and 912) under *C. clavata* without listing *C. ecklonii* var. α in the synonymy. Kükenthal's description of *C. extensa* var. *ecklonii* resembles much more the one of var. β than var. α.

I therefore regard *C. ecklonii* Nees var. β as the true *C. ecklonii,* as the name is commonly applied to material which resembles the Mundt material. The species is distinct from other African material by the small, no more than 3 cm long spikelets, the 4-5 mm long utricles (vs. min 3 cm long spikelets and 5-6 mm long utricles in *C. clavata*), which abruptly narrows into the 1mm long beak (vs. gradually tapering into the 1.25-1.5 mm long beak in *C. monotropa*) and distinct teeth (vs. no teeth in *C. burchelliana*)

C. ecklonii Nees is sometimes cited as a synonym of *S. ecklonii* Nees which is present in the Eastern Cape near Port Elisabeth. However, *C. ecklonii* clearly belongs to *Carex* and not *Schoenoxiphium* since the utricles are entirely closed, the rachilla inconspicuous and florets (= spikelets) either entirly male or female.

***Carex humberti* Cherm.**

Bull. Soc. Bot. France. 73: 554-555 (1926). Type: Madagascar, Andringitra Mts. (Iratsy): Riambava valley and Antsifotra and surrounding area, Nov.-Dec. 1924, *H. Humbert* 3745 (holo. P).

Habitat: forest or wet slopes

Distribution: Madagascar (Andringitra Mts.), 2000 m

Notes: *C. humberti* is distinct from other *Carex* species from Madagascar by the unique combination of ca. 6 mm long, utricles with a distinct rostrellum and teeth and the long and thin, pendulous spikelets.

***Carex johnstonii* Boeckeler**

Bot. Jahrb. Syst. 7: 278 (1886). Type: Tanzania, Kilimanjaro, 2000 – 3300 m, *H.B. Johnston* (holo. B†; iso. K).

C. volkensii K.Schum. in Engl. Pflanzenw. Ost -Afr. C: 130 (1895). Type: Tanzania, Kilimanjaro, above Marangu, Kifinka-Lager 2200 m, *G. Volkens* 1124 (holo. B†; iso. K).
C. kuekenthalii K.Schum. ex C. B. Clarke, Bot. Jahrb. Syst. 38: 136 (1906), nom. illeg. non Dörfl. ex H.Zahn, Oesterr. Bot. Z. 50 : 106 (1900). Type: Ethiopia, 3100 m, *Neumann* 35 (Type locality not found).
C. johnstonii Boeckeler var. *angustifolia* Cherm. Bull. Soc. Bot. France 82: 343 (1935). Type: DR Congo, 1929/6, H. Humbert 8655 (BR).
C. johnstonii Boeckeler var. *brevifructus* Kük. Protolog not found, on material Southern Tanzania, Mbeya region, Rungwe District, near Kyimbila station, 1600-1800 m, 06. June 1912, Stolz 1331 (UPS, Z).

Habitat: forest understory and forest edge 1500-3300(-3600) m

Distribution: Ethiopia, Kenya, Uganda, DR Congo, Rwanda, Malawi

Note: *C. johnstonii* is a very variable species and several colour forms exist, ranging from dark red to yellow lower leaf sheath and utricles from brown to light green. Kükenthal seem to have annotated some southern Tanzanian material as a distinct variation: *C. johnstonii* Boeckeler var. *brevifructus* Kük. Verdcourt (pers. com.) came to a similar conclusion but did not mention var. *brevifructus.* However, the colour and hairiness can vary widely in this species, consequently more material should be studied before recognising infraspecific taxa.

***Carex longipedunculata* K.Schum.**

Engl. Pflanzenw. Ost -Afr. C: 130 (1895). Type: Tanzania, Kilimanjaro, swampy ditch near Noholu cave, 3200 m, 1893, *G. Volkens* 2015 (B).

C. longipedunculata K.Schum. var. *longistipitata* Kük. Notizbl. Bot. Gart. Berl. 9: 316 (1925) Type: Kenya, Western part, *Hagenia*-zone, 3100 m, 30.-31. Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 1300 & 1300a (syn. UPS).

C. longipedunculata K.Schum. f. *recedens* Kük. protolog not found Type: DR Congo, Hagenia forest on Karisimbi Volcano, N.E. Kiwu, 11-1907, *J. Mildbraed* 1578 (K).

C. fischeri K.Schum., Engler Pfl. Ost-Afr. C: 130 (1895). Type: Kenya, Mau Escarpment, Abori, *Fischer* 640 (K).

Habitat: wet places in forest

Distribution: Kenya, Uganda, Congo, Rwanda, Northern and Southern Tanzania, Malawi

Note: Very similar to other members of section *Elatae* Kük. from Africa, e.g. *C. boryana, C. humberti,* C. *ninagongensis, C. simensis* and *C. vallis-rosetto.* Distinct by the utricles (5-6 mm long), spikelets always single, leaf base yellow, brown or orange, but never red as in other members in the section.

***Carex madagascariensis* Boeckeler**

Bot. Jahrb. Syst. 5: 517 (1884). Type: Madagascar, Andrangoloaka, in swamps, Nov. 1880, *J.M. Hildebrandt* 3753 (syn. P, M, Z).

Habitat: swamps at forest edges, 700-1600 m

Distribution: Central and East Madagascar

Note: *C. madagascariensis* is very similar to C. *papillosissima* from Southern Tanzania differing by the slightly less densely papillous utricles. It also resembles *C. baronii* from Madagascar and *C. austro-africana* from Southern Africa, differing from *C. baronii* by the absence of distinct veins on the utricles (vs. veins present and distinct in *C. baronii*) and from *C. austro-africana* by the utricles which are more densely papillous and the awn of the pistillate scales which is not longer than the utricle (vs. utricles with few papillae and pistillate scales with an awn which is much longer than the utricle).

***Carex mannii* E.A.Bruce**

Bull. Misc. Inform. Kew: 150 (1933). Type: Fernando Po, Clarence Peak, *Mann* 1478 (holo. K; iso. K).

C. boryana Schkuhr var. *simplicissima* Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 651 (1909) p.p. (see also *C. boryana* and *C. vallis-rosetto*). Syntypes: Fernando Po, Clarence Peak, *Mann* 661 (syn. K). Fernando Po, Clarence Peak, *Mann* 1478 (syn. K). Uganda, Rwenzori Mts., *Scott-Elliott* 7873 (syn. K) La Réunion, *Boivin* 997 (syn. P).
C. boryana Schkuhr var. *minor* Boott Illustr. III, partim, quoad t. 348. (1862). Type not indicated.

Habitat: wet places in the shade or openings in the forest

Distribution: W. Cameroon, Fernando Po and possibly Eastern Africa

Note: Bruce described *C. mannii* as being similar to *C. boryana.* Haines and Lye (1983) state that *C. mannii* is related to *C. simensis*, which has darker and more abruptly subulate pistillate scales with pale midribs, and *C. petitiana*, which normally has single spikes from the leaf-sheaths. *C. mannii* is the only one of these three species which has male flowers above in some spikes. In *C. mannii* the length of the pistillate scales and utricles is very variable. It is also closely related to *C. vallis-rosetto*, distinguished by spikelets which are usually no more than 6 times as long as wide in *C. mannii* opposed to more than 6 times as long as wide in *C. vallis-rosetto.*

***Carex monotropa* Nelmes**

Bull. Misc. Inform. Kew 10: 86 (1955). Syntype: Lesotho, Mont-aux-Sources, 2 850 m, Jan 1894, *Flanagan* 2013 (holo. K; iso. BM, K, NU, PRE). Type: Lesotho, between Indumeni Dome and Castle Buttress, common in moist parts of alpine grassland, 2910 m, 05 Dec.1952, Killick 1847 (syn. K, NU, PRE).

Habitat: Plants grow in wet, turf-like vegetation or in bare gravel patches.

Distribution: endemic to Drakensberg summit plateau

Notes: Probably closely related to *C. flava* L. from Europe.

***Carex mossii* Nelmes**

Bull. Misc. Inform. Kew: 137 (1940). Type: South Africa, Eastern Cape Province, Hogsback, 1 Jan. 1927, *C. E. Moss* 999 (holo. K; iso. BM).

Habitat: wet places along streams, shaded places in forest

Distribution: South Africa: Natal, Midlands, Uplands

Notes: Spikes of *C. mossii* are elongate markedly with maturity. It is closely related to *C. bequaertii* and difficult to distinguish but seems to be smaller. Also close to *C. penduliformis* from Madagascar and C. *pendula* Huds. from Europe.

Notes: Very closely related to *C. penduliformis* and *C. bequaertii* (see notes under these species).

C. *ninagongensis* (Kük.) Nelmes ex Robyns & Tournay

Fl. Spermatophyt. Parc Nat. Albert 3: 292 (1955). *C. longipedunculata* K.Schum var. *ninagonensis* Kük. Notizbl. Bot. Gart. Berl. 9: 316 (1925). C. *simensis* Hochst. ex A.Rich. var. *ninagongensis* (Kük.) Kük. Notizbl. Bot. Gart. Berl. 9: 316 (1925). Type: Rwanda; Kissenye (Ninagongo, Nyiragongo), 16 April 1907, *J. Mildbraed* 1338 (K).

C. fischeri K.Schum. var. *basiandra* Kük. Notizbl. Bot. Gart. Berl. 9: 315 (1925). Syntypes: Kenya, Western Kenya, 3. Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 659a (syn. UPS). Kenya, Mt. Kenya, Liki River, 11. Feb. 1922, *Rob.E.Fries & Th.C.E.Fries* 1462 (syn. K, UPS). Kenya, Aberdare Mts., 12. March 1922, *Rob.E.Fries & Th.C.E.Fries* 2210 (syn. K, UPS). Kenya, Mt. Elgon, in bamboo zone, *R.A. Dummer* 3465 (type locality unknown).

C. longipedunculata K.Schum var. *lanuriensis* DeWild. Pl. Bequaert. 4: 247 (1927). C. *simensis* Hochst. ex A.Rich. var. *lanuriensis* DeWild. Pl Bequaert. 4: 247 (1927). Syntypes: DR Congo, Rwenzori Mts., Lanuri Valley 4.000-4.300 m, *Bequaert* 4680 & 4520 (syn.BR, K, S); ibid. 3000 m, (syn. BR, PRE).

Habitat: forest amongst rocks or at the edge of grassland

Distribution: Kenya, Uganda, Tanzania, possibly also DR Congo and Rwanda

Note: This is not a very commonly recognised species. Haines and Lye (1983) have sunk it into *C. petitiana* and Verdcourt (pers. com.) follows their opinion. Nevertheless, the two differ in the more than 10 times longer and thinner spikelets and dark red leaf base of *C. ninagongensis* make it a distinct species (*C. petitiana* has brown or yellow leaf bases, spikelets less than 6 times as long as wide).

***Carex papillosissima* Nelmes**

Bull. Misc. Inform. Kew: 158 (1939). Type: Tanzania, Iringa Province, Sao Hill, ca. 1800 m, 27 Oct. 1936, *Staples* 416 (holo. K; iso. EA).

Habitat: in open upland forest around 1700 m.

Distribution: *C. papillosissima* is very rare, only known from type locality. it was not found during a brief visit of the area by the author in 2005. The area is intensely used for agro-forestry and the species might therefore be extinct.

Note: *C. papillosissima* is very similar to *C. madagascariensis* and other members of the Section *Praelongae* Kük. from Africa (i.e. *C. austro-africana*) which have distinct utricles without teeth and an inconspicuous rostrellum. *C. papillosissima* is distinct from the other by the broad leaves (4-10 mm wide), dense papillae on the utricle and the longer (3-4 mm long) and narrowly lobed pistillate scales (see also notes under *C. madagascariensis* and *C. austro-africana)*

***Carex penduliformis* Cherm.**

Bull. Soc. Bot. France 70: 414 (1923). Syntypes: Madagascar, Centre, Andasibé forest (Onive basin), 1912, *H. Perrier de la Bâthie* 2535 (syn. P) Madagascar, Centre, Andringitra Mts., 1922, *H. Perrier de la Bâthie* 14554 (syn. P).

Habitat: humid forest understory, 1400-1800

Distribution: Central Madagascar

Notes: Very similar to *C. bequaertii* and *C. mossii* and difficult to distinguish but flowers not as dense and pistillate scales shorter than utricles (no more than 3 mm long).

***Carex petitiana* A.Rich.**

Tent. Fl. Abyss. II: 513 (1851). Type: Ethiopia, *Petit* s.n. (holo. P).

C. anomala Steud. Syn. Pl. Glumac. 2: 230 (1855) none of Pall. (1808) non Boott.
C. elgonensis Nelmes, Bull. Misc. Inform. Kew: 245 (1938). Type: Kenya, Mt Elgon, 3 240 m, 20 Feb 1935 *Taylor* 3474 (holo. BM).

C. mildbraediana K.Schum. var. *friesiorum* Kük. Notizbl. Bot. Gart. Berl. 9: 314 (1925). cited in Monocots Checklist incorrectly as Engler (ed.), Pflanzenr., IV, 20(38): 767 (1909). Type: Kenya, Mt. Elgon, 28. Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 1228 (syn. UPS). Kenya, Aberdare Mts. eastern side in bamboo zone, 2700 m, 31. March 1922, *Rob.E.Fries & Th.C.E.Fr*ies 2553 (syn. UPS). Kenya, Aberdare Mts., Kinangop, 15. March 1922, *Rob.E.Fries & Th.C.E.Fries* 2652 (syn. UPS).Kenya, Aberdare Mts., Kinangop, 2. April 1922, *Rob.E. & Th.C.E.Fries* 2703 (syn. B, UPS).
C. mildbraediana K.Schum. var. *alpicola* Kük. Notizbl. Bot. Gart. Berl. 9: 315 (1925). Type: Kenya, Aberdare Mts., wet places in the alpine region, 19. March 1922 Kenya, *Rob.E. & Th.C.E.Fries* 2671 (UPS).
C. vallis-rosetto K.Schum. var. *heterostachya* Kük. Notizbl. Bot. Gart. Berl. 9: 314 (1925). Type: Kenya, West Kenya Forest Station, Mt. Aberdare, 05 Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 769 (syn. BR, K, UPS).

Habitat: grassland

Distribution: Ethiopia, Kenya, Uganda, probably Northern Tanzania

Note: The original description cites only material from Petit (Ethiopia, without collection number or date). Kükenthal mentions *Schimper, Dillon* and *Steudner* collection from Ethiopia as well as material from South Africa. The drawing on page 425 and probably those from Boott refer to these South African collections which belong mostly to *C. mossii* Nelmes. This species lacks a distinct rostrellum and does not have teeth. As the description of Kükenthal and others citing him state that *C. petitiana* has no teeth, thus considerable confusion has arisen about the status of the species. Durand (1894) only cites *Schimper* 1038, while Engler (1895) and Nelmes (1940) refer to *Schimper* 100 as the type.

Nelmes (1940: 135) stated that the examined type material was found to consist of two very distinct species. “Only one specimen of the some half dozen on the Type sheet represents the plant which has been known as *C. petitiana* by every authority on the Cyperaceae since the publication of the name in 1851. This specimen consists of but a single flowering culm without its basal portion. An analysis of the description of *C. petitiana* shows that this significant portion of the plant material clearly referred to by only about one tenth part of the essential points. The overwhelming part, therefore, of both the material and its description, including the key portion, belongs to another species. This, therefore, I submit, is the true *C. petitiana* A. Rich. It is intermediate between *C. longipedunculata* K.Schum. and *C. cuprea* (Kük.) Nelmes [...] “ He might have meant by "type material" the collections cited by Kükenthal (1909) as the type sheet of the single collection cited by A. Richard in the protologue of *C. petitiana* is present only in P. A number of names usually placed in synonymy *C. petitiana* actually refer to material of other species such as *C. pendula* Huds. sensu C.B.Clarke which represents material of *C. bequaertii*.

C. petitiana as described by A. Rich. on material of Petit is possibly not distinct from *C. elgonensis* Nelmes or *C. mildbraediana* Kük. var. *friesiorum* Kük. and differences to the West African species *C. mannii* E.A. Bruce are small. Haines and Lye (1983) stated that *C. petitiana* and *C. elgonensis* differ in *C. elgonensis* having darker spikelets and scales. I think the colour difference is not sufficient to recognise *C. elgonensis* as a separate species.

***Carex phragmitoides* Kük.**

Fedde Repert. 21: 329 (1925). Type: Tanzania, edge of the Ossirwa crater lake, 13 Feb. 1907, *F. Jaeger* 446, (holo. B; frag. K).

C. taylori Nelmes Bull. Misc. Inf. Kew.: 472 (1937). Type: Kenya, Aberdare Mountains, Mt. Kinangop, in marsh, 27. Oct. 1934, *G. Taylor* 13354a (holo. BM and K utricles from type material).
C. abyssinica Chiov. in Ann. Bot. Roma 9: 150 (1911). *C. cognata* Kunth. var. *abyssinica* (Chiov.) Lye. Nordic J. Bot. 3(2): 244 (1983). Type: Ethiopia, Simien, Debarek near stream, 11 July 1909, *Chiovenda* 960 (holo. FI; K fragments).

Habitat: upland bogs and marshes, streamside or other wet places, 2500-3100 m

Distribution: Southern Ethiopia, Kenya and Northern Tanzania

Notes: *C. phragmitoides* is rare. It can be distinguished from other species with crowded spikelets (i.e. *C. sp. A* or *C. sphaerogyna* from Madagascar) by the long scabrid awn on the pistillate scale and the fine hairs on the utricle (see also notes under *C. sp. A* and *C. ecklonii*).

***Carex preussii* K.Schum.**

Bot. Jahrb. Syst. 24: 340 (1897). *C. longipedunculata* var. *preussii* (K.Schum.) Kük. Bull. Misc. Inform. Kew: 247 (1933). Type: Mt. Cameroon, near Mann's spring, 2600 m, 4 Feb. 1891, *Preuss* 727 (B).

C. preussii var. *camerunensis* Nelmes Bull. Misc. Inform. Kew: 247 (1938). Type: Cameroon, Mt. Cameroon, Dec.1862, *G. Mann* 2099 (lecto. K).

Habitat: Montane grassland

Distribution: Nigeria and Western Cameroon (Gotel Mts., Mambila Plateau, Mt. Cameroon)

Notes: Nelmes (1938) stated that Kükenthal was wrong in placing *C. preussii* as a variety of *C. longipedunculata* K.Schum. and states that this might be due to the poor specimens of *C. preussii* in Berlin. Nelmes describes in the same article the variation *camerunensis* Nelmes which was cited by Kükenthal (1909: 654) as *C. simensis*. Here it is maintained as a separate species, although it is very similar to *C. longipedunculata* and the status needs assessment.

***Carex renauldi* H.Lév.**

Cat. Pl. Yunnan: 289 (1917). *C. lebrunei* H.Lév. Bull. Acad. Int. Géogr. Bot. 27: 4 (1917), nom. illeg. non H.Lév. in Monde des Pl., 17:15 (1915). Type: Madagascar, Centre, Manankazo northeast of Ankazobé, Nov. 1913, *H. Perrier de la Bâthie* 2711 (P).

Habitat: along streams, wet places in forest, 1500-2400 m

Distribution: Central Madagascar

Notes: *C. renauldi* is easily recognised by the unique combination of the small size (30-70 cm tall), narrow leaves (1.5-2 mm wide), the presence of only a few florets and the long utricles (7-9 mm long).

***Carex simensis* Hochst. ex A. Rich.**

Tent. Fl. Abyss. II: 514 (1850). Type: Ethiopia, Simien, Mt. Buahit, *W. Schimper* 1180 (holo. P; iso. BM; K, M, S, UPS, Z).

C. simensis Hochst. ex. A. Rich. var. *longistipitata* Kük. Notizbl. Bot. Gart. Berl. 9: 316 (1925). Syntype: Kenya, Mt Kenya, W. slope 2800 m, *Rob.E.Fries & Th.C.E.Fries* 1300 (syn. BR; K; S; UPS); 1300a (syn. UPS).
C. simensis Hochst. ex. A. Rich. var. *nemorum* Chiov. Bull. Jard. Bot. Buitenzorg, ser. 3.: 383 (1912). Type: Ethiopia, Scioa, Mt. Entotto, 2600 m, 27. April 1909, *G. Negri* 333 bis. (R? type location not indicated)
C. karisimiensis Cherm. Bull. Soc. Bot. France 82: 344 (1935). Syntypes: DR Congo/Uganda, Mt. Muhavura, 3500 m, June 1929, *H. Humbert* 8518 (P). DR Congo, Mt. Karisimbi, 3400-3800 m, June 1929, *H. Humbert* 8557 (syn. B, BR, P).

Habitat: moist places in forest and grassland, from the upper part of the montane belt into the alpine belt (2450-3950 m)

Distribution: Ethiopia, Kenya, Northern Tanzania (Kilimanjaro), Uganda, DR Congo

Note: A number of variations have been described (*C. simensis* Hochst. Ex. A. Rich. var. *lanuriensis* De Wild.; var. *longistipitata* Kük.; var. *mauensis* Kük.; var. *stolonifera* (Boeckeler) Kük. (= *C. cuprea*); var. *ninagonensis* (Kük.) Kük. Nelmes stated (1938:246) that the specimen of Mann 2099 from West Africa that is cited by Kük. as *C. simensis* is *C. preussii* K.Schum. var. *camerunensis*, on which I agree. Both Haines and Lye (1983) and Verdcourt (pers. com.) key out the species by lateral spikelets arising in pairs, although most of the type sheets have only spikelets araining singly. A better character with which to distinguish *C. simensis* from other species are the dark pistillate scales which contrast with the green utricles in combination with the coriaceous, rigid leaves and the 6-7 mm long utricles. Material with shorter utricles belong in my opinion to *C. ninagonensis*. *C. simensis* has 1-2 terminal male spikelet present, the lower male spikelet often with female flowers in the upper half of the spikelet, sometimes a few male flowers at the base of each female spikelets present, female spikelets more commonly arising single than in pairs. *C. petitiana* has no exclusively spikelets which are only male and spikelets always arise singly.

Carex sp. A.

C. cognata sensu Haines and Lye The sedges and rushes of East Africa: 383 (1983), sensu Lye Fl. Ethio. & Eritr.: 510 (1997) non Kunth Enum. Pl. 2: 502 (1837).
C. pseudocyperus L. var. *cognata* (Kunth) Boott, *Carex* 4: 141 (1867). Type not indicated.
C. cognata Kunth. var. *congolensis* (Thurrill) Lye Nordic J. Bot. 3(2): 244 (1983). *C. congolensis* Thurrill. Bull. Misc. Inform. Kew: 240 (1912). Type: DR Congo, Katanga, Lubumbashi (Elisabethville) 11°37'S, 27°24'E, 1150 m, 21. Oct 1911, *F.A. Rogers* 10 082 (holo. K).
C. acutatiformis Hess, Ber. Schweiz. Bot. Ges.: 355 (1935). Angola, 4 km east of Rio Cutato, next to the road to Vila Serpa Pinto, 1400 m, 15. Jan 1952, *Hess* 52/224 (Z Hess collection).
C. pseudo-sphaerogyna Nelmes Bull. Misc. Inform. Kew: 473 (1937). Type: Uganda, Kigezi Distr., Virunga Mts., on margin of swamp, 27. Nov. 1934, *Taylor* 2146 (Type locality not indicated).

Habitat: moist places in running or standing water or wet grassland, near seepages, 1600-3000 m

Distribution: Eastern to Southern Africa from Uganda to the Drakensberg not known from Kenya or Tanzania but present in Angola, Botswana and Swaziland. Records from the Western Cape Province in South Africa are due to misapplications of the name.

Note: *C. sp. A* is a widespread species formerly recognised as *C. cognata* Kunth. However, the type of *C. cognata* is part of the type material of *C. ecklonii* (var. β). The name *C. cognata* Kunth. is therefore the later one and invalid (see discussion under *C. ecklonii* and *C. drakensbergensis*). Two varieties of *C. sp. A* (= *C. cognata*) have been proposed. Haines and Lye recognised a var. *abyssinica*. This has been placed in synonymy with *C. phragmitoides*. Haines and Lye also distinguished var. *congolensis* but characters are not consistent enough to separate the material. The treatment presented here is in accordance with Maquet (Fl. Rwanda 3 (1988): 429 and Verdcourt, pers. com.), with the exception that *C. drakensbergensis* is considered a distinct species: it differs by the 5-8 mm long spikelets (in *C. sp. A* spiklets are 2-3(-4) mm long), the utricles which are not inflated at maturity (*C. sp. A* has utricles distinctly inflated at maturity) and longer, 1mm long, finer teeth (*C. congolensis* has teeth 0.5-0.8 mm long).

Carex sphaerogyna Baker

Journ. of Bot. 21: 129 (1883). Syntypes: Madagascar, Central-Madagascar, Andrangoloaka, in swamp, Nov. 1880, *J.M. Hildebrandt* 3754 (syn. M, Z); Madagascar, Central-Madagascar, *R. Baron* 2040 (syn. P).

Habitat: In wet places, water seapages or along rivers at high altitudes

Distribution: Madagascar

Notes: The two collections from the type material are very different. The material from Hildebrandt is unusual, the leaves are lax and smaller than the usual material from *C. sphaerogyna*, which usually has very rigid leaves. Another variation has been described, *C. sphaerogyna* var. *brasiliensis* H.Pfeiff., Repert. Spec. Nov. Regni Veg. 17: 32 (1921) presumably from Brazil.

***Carex subinflata* Nelmes**

Bull. Misc. Inform. Kew: 270 (1940). Type: South Africa, Eastern Cape Province, Barkly East, Doodman's Krans Mountains, 2600 m, 7 March 1904, *Galpin* 6882 (holo. K).

Habitat: In bogs, wet flushes or along rivers at high altitudes (± 2800 m), usually in full sun.

Distribution: Eastern side of Southern Africa

Note: *C. subinflata* is similar to *C. clavata* but generally smaller, with erect or suberect spikelets 2-4 cm long ± 8 mm diameter, pistillate scales 3-5 mm long, shorter than the utricles (including the awn), utricles 4.5-5.5 mm long, dark reddish-brown, as opposed to erect spikelets 2-8 cm long, (8-)10-15 mm wide and utricles 6-7.5 mm long in *C. clavata*. Gordon-Gray (1995: 43) states that this species is close to *C. drakensbergensis* (mentioned as *C. cognata*, see also under *C. sp. A*), *C. drakensbergensis* has only pendulous spikelets opposed to erect ones in *C. subinflata.*

***Carex sylvatica* Huds.**

Fl. Angl.: 353 (1762).

Note: Identified by Reid on material collected in South Africa, probably introduced from Europe.

***Carex thomasii* Nelmes**

Bull. Misc. Inform. Kew: 245 (1938). Type: Sudan, Imatong Mts., Lomuleng, forest, common, 2400 m, 29 Dec. 1935, *Thomas* 1794 (K).

Habitat: in upland forest

Distribution: only known from the Imatong Mts., but might also occur in Uganda.

Note: It is sufficiently difficult to discern *C. thomasii* from *C. petitiana* that it might be better to reduce *C. thomasii* to synonymy of *C. petitiana*.

***Carex vallis-rosetto* K.Schum.**

Engl. Pflanzenw. Ost -Afr. C: 130 (1895). Type: Tanzania, Usambara, Rosetto valley, C. Holst 3823 (hololecto. B; iso. K).

C. mildbraediana Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 767 (1909). Type: Tanzania, Rukarara, Rugege Wald, fountain in swamp, 1800 m, Aug. 1907, *J. Mildbraed* 966 (holo. B; K fragments).
C. ramosipes Cherm., Bull. Soc. Bot. France 82: 343 (1935). Type: DR Congo, Kivu Distr., Mt. Ninagong, March 1929, *H. Humbert* 7939 (holo. P).
C. boryana Schkuhr var. *simplicissima* Kük. in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 651 (1909) p.p. (see also *C. boryana* and *C. mannii*). Syntypes: Fernando Po, Clarence Peak, *Mann* 661 (syn. K). Fernando Po, Clarence Peak, *Mann* 1478 (syn. K). Uganda, Rwenzori Mts., *Scott-Elliott* 7873 (syn. K) La Réunion, *Boivin* 997 (syn. P).
C. cyrtosaccus C.B.Clarke Fl. Trop. Afr. 8: 524 (1902), Type: Malawi, Mt. Mlanji, 1891, *Whyte*, s.n. (lecto K) other material mentioned in protolog: Malawi, Mt. Malosa, *Whyte* s.n. (K) and Zomba, *Whyte* s.n. (K).
C. vallis-rosetto K.Schum. var. *purpurea* Kük., in Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 647 (1909). Syntypes: Tanzania, Mt. Kilimanjaro, at the foot of Kipinika, Nov. 1893, *G. Volkens* 1342 (type locality not known). Tanzania, Mt. Kilimanjaro, Marangu, Dec. 1893, *G. Volkens* 1291 (type locality not known).
C. vallis-rosetto K.Schum. forma *ramosa* Kük. Notizbl. Bot. Gart. Berl. 9: 314 (1925). Syntypes: Kenya, Mt. Kenya, Western part of Mt. Kenya, in mountain forest 2350 m, 3. Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 676 (syn. UPS). Kenya, Mt. Kenya, West Kenya Forest Station, 22. Jan. 1922, *Rob.E.Fries & Th.C.E.Fries* 1158 (syn. UPS).
C. greenwayi Nelmes Bull. Misc. Inform. Kew: 244 (1938). Type: Tanzania, Bismarck Hill, damp places, with ferns, in dense shade of *Phillipia excelsa*, *Hagenia abyssinica* and *Podocarpus* forest and woodland, 3000 m, 27. Feb. 1934, *P. Greenway* 3840 (BR).

Habitat: damp places, in the shade

Distribution: Kenya, Tanzania, Uganda, DR Congo

Note: Lectotypification was by Nelmes (1938: 243) in which he stated that the three sheets (C. Holst, no. 3823; G. Volkens 1291 and 1342) mentioned by K.Schum. seem to represent two, if not three, different species, and that the description does not fit any one of them better than the others. He assigned Holst 3823 to be the lectotype because (1) it was the only specimen collected in the Rosetto valley (2) it was chosen as lectotype by Kükenthal (1909: 647) where the two Volkens sheets were listed under var. *purpurea*. Nelmes included Volkens 1342 in *C. greenwayi* which he described as a new species but which was

reduced into synonymy of *C. vallis-rosetto* by Haines & Lye (1983). We follow their treatment, although the material of *C. greenwayi* has partly single spikelets arising from the bracts and needs a more careful investigation. *C. mildbraediana* and *C. cyrtosaccus* are also treated as synonyms of *C. vallis-rosetto* here, as their diagnoses are based on characters (i.e. the occurrence of lateral branching spikelets and bent utricles) which we consider unreliable.

SUBGENUS INDOCAREX Nelmes / SECTION VIGNEASTRA

The subgenus *Indocarex* is easily recognised by the bisexual spikes arranged in open branched panicles and a prominent prophyll that resembles a utricle at the base of an inflorescence branch. All species prefer lower altitudes than the members of the other subgenera and can even be found in *Brachystegia* woodland at 1500 m altitude in East Africa. There are about 25 species of *Indocarex* in Tropical and Southern Africa and 15 species in Madagascar distributed at mid-elevation in the highlands throughout the continent from Nigeria to Malawi and from Ethiopia to South Africa and Angola.

The species are both relatively similar on to another and often morphologically heterogeneous (even within individual specimens). Further research in this group is necessary: it may yet be concluded that it is more useful to recognise fewer species than those listed here. When investigating species of *Indocarex* one should always pay careful attention the different parts of the inflorescence, as distribution of hairs and the size of flower parts differ throughout the ontogenetic stages of the inflorescence.

The key is divided into two parts, the first, a new key for species from continental Africa and a second key for species of Madagascar, which is a translation of the key from Chermezon from the Flora of Madagascar (1923) with a few changes.

Key of *Indocarex* from continental Africa:

1. Pistillate scales (3-) 5-6 mm long, utricles 5-7 mm long ..... 2.
1* Pistillate scales 3-6 mm long, utricles 3.5-4.5 (-5) mm long ..... 7.

2. Utricles 5-7 mm long, very gradually narrowing into the 1.5-2.2 mm long and slender rostrellum ..... 3.
2* Utricles 5-6 mm long, more or less gradually narrowing into the 1-1.5 mm long rostrellum ..... 4.

3. Panicles dense, leaves coriaceous, (3)5-12 mm wide, utricles 5-6 (-7) mm long, rostrellum 2 mm long scabrid, pistillate scales (3-) 5-6 mm long, leaf base brown or yellow ..... *C. steudneri*
3* Panicles spreading, leaves chartaceous, (2-)5-9 mm wide, utricles 4-5.5 mm long, rostrellum 1.5-2.2 mm long, glabrous or scabrid, s pistillate cales 4-5 mm long leaf base green, yellow or brown (see also *C. schliebenii*) ..... *C. chlorosaccus*

4. Leaves 5-11 mm wide, utricles 4-5 mm long, pistillate scales 5-6 mm long, leaf base dark reddish or dark brown..... 5.
4* Leaves 3-5.5 mm wide, utricles 5-6 mm long, pistillate scales 4-6 mm long, leaf base yellowish or brown to slightly reddish ..... 6.

5. Leaves 5-8 mm wide, leaf base dark reddish, utricles 4-5 mm long, rostrellum 1-1.5 mm long scabrid, pistillate scales 5-6 mm long, ... *C. angolensis*
5* Leaves 8-11 mm wide, leaf base brown or yellowish, utricles 5 mm long, rostrellum 1.5 mm long, scabrid, pistillate scales 5-5.5 mm long ..... *C. tricholepis*

6. Leaves 3-4 mm wide, leaf base dark brown to slightly reddish, pistillate scales 4-5 mm long, utricles 5-5.5, rostrellum glabrous or scabrid, 1 mm long,..... *C. brassii*
6* Leaves 3-5.5 mm wide, leaf base dark brown, pistillate scales 5-6 mm, utricles 5.5-6 mm long, rostrellum 1-1.5 mm long scabrid, teeth long ..... *C. macrophyllidion*

7. Leaves 1.5-4(-5) mm wide, utricles 3.5-4 mm long ..... 8.
7* Leaves (5-)6-14 mm wide, utricles (3.5-) 4-5 mm long ..... 11.

8. Leaves 1.5-2 mm wide, leaves rolled, dark green, leaf base dark red (Southern Tanzania) ..... *C. schliebenii*
8* Leaves 3-5 mm wide, leaf base dark red or brown, leaves flat (West Africa, Angola) ..... 10.

9. Leaves 3-4 mm wide, leaf base brown, utricles 4 mm long, rostrellum scabrid, 1.5-2 mm long (West Africa)..... *C. neo-chevalieri*
9* Leaves 3-5 mm, leaf base brown or reddish, utricles 3.5-4 mm long, rostrellum with fine hairs (Angola) ..... *C. humpatensis*

10. Leaves 12-14 mm wide, inflorescence up to 45 cm long, dark, scales dark red, tricles scabrid with distinct, long hairs (Kenya, Tanzania) ..... *C. castanostachya*
10* Leaves 5-15 mm wide, inflorescence 2-20cm, scales green, yellow, brown or slightly reddish, utricles glabrous or shortly scabrid ..... 11.

11. Panicle with 3-4 spiklets, leaves 5-8 mm wide, pistillate scales 4.5-5 mm long, utricles 4.5-5 mm long, with a 1.5-2 mm long rostrellum, entirely covered in dense,fine hairs, with a leaf base brown to dark red (South Africa) ..... *C. merxmuelleri*
11* Panicle with more than 4 spiklets, leaves 5-14 mm wide, pistillate scales 3-6 mm long with or without a awn, utricles 3-6 mm long, with a 0.5-2 mm long rostrellum, glabrous or entirely covered in dense, fine hairs, leaf base red, brown or yellow ..... 12.

12. Utricles 3.5-4 mm long, rostrellum scabrid, pistillate scales brown to dark brown, 3.5-4 mm long, leave base brown ..... *C. spicato-paniculata*
12* Utricles 3.5-5 mm long, rostrellum scabrid or glabrous, pistillate scales green, light brown or yellowish never dark brown ..... 13.

13. Leaves 5-9 mm wide, utricles 4-5.5 mm long, gradually narrowing into the 1.5-2.2 mm long glabrous or scabrid rostrellum (Northern and Eastern Africa) ..... *C. chlorosaccus*
13* Leaves 3-5 mm, leaf base brown or reddish, utricles 3.5-4 mm long, rostrellum with fine hairs..... 14

14. Teeth prominent, 0.5-1 mm long (Eastern, North-eastern and West Africa) ..... 15. *C. echinochloe*
14* Teeth prominent, 0.2-0.5-1 mm long (Angola, Zimbabwe and Malawi) ..... 16.

15. Leaves 6-14 mm wide, utricles 3.5-4 mm long, rostrellum 1 mm long scabrid, pistillate scales 4-5 mm long, awn 1-2 mm (Eastern, North-eastern and West Africa) ..... *C. echinochloe* subsp. *echinochloe*

15* Leaves 5-10 mm wide, utricles 4-4.5 mm long, rostrellum 1 mm long, slightly scabrid, pistillate scales 4-5 mm (Malawi, Southern Tanzania). ..... *C. echinochloe* subsp. *nyasensis*

16. Leaves 5-8 mm wide, utricles 4-5 mm long, rostrellum 1-1.5 mm long, pistillate scales 5-6 mm long, leaf base dark reddish ..... *C. angolensis*

16* Leaves 8-11 mm wide, utricles 5 mm long, rostrellum 1.5 mm long, pistillate scales 5-5.5 mm long, leaf base brown or yellowish ..... *C. tricholepis*

***Carex angolensis* Nelmes**

Bull. Misc. Inform. Kew: 162 (1940). Type: Angola, District of Moxico, between R. Monu and R. Kampashi in Brachystegia woodland, on sand, 19. Jan. 1938, *E.W.B.H. Milne-Readhead* 4222, (holo. K).

Habitat: in Brachystegia woodland

Distribution: Angola, Zimbabwe, Zambia

Notes: *C. angolensis* has pistillate scales which are much shorter than the utricle (usually just reaching the rostrellum), utricles green and inflated, rostrellum slender, slightly flattened with 5-7 distinct veins. Spikelets well separated. Possibly not distinct from *C. echinochloe* subsp. *nyasensis*, although Nelmes stated that it differs in secondary panicles more pyramidal and distant. Differs only slightly from *C. tricholepis* in the narrower leaves (5-8 mm wide and leaf base dark reddish, opposed to 8-11 mm wide leaves and brown or yellowish leaf base in *C. tricholepis*).

Carex brassii Nelmes

Mem. N.Y. Bot. Gard. 9: 100 (1954). Type: Malawi, Mt. Mlanje, Luchenya Plateau, 1890 m, 07. July 1946, *L.J. Brass* 16714 (holo. K; iso. BM, BR, PRE).

Habitat: along streams in forest

Distribution: Southern Malawi, only known from Mt. Mlanje

Notes: *C. brassii* is, according to the Nelmes (1954), similar to *C. spicato-paniculata* and *C. chlorosaccus*. However, it resembles much more *C. tricholepis* and *C. angolensis,* differing in the narrower, 3-5.5 mm wide, leaves, 5-6 mm long utricles, pistillate scales 4-6 mm long, opposed to *C. tricholepis* and *C. angolensis* with broader, 5-11 mm wide, leaves, 4-5 mm long utricles, pistillate scales 5-6 mm long in.

***Carex castanostachya* K.Schum.**

Kük. Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 276 (1909). Type: Tanzania, Uluguru Mts., forest edge at 2300 m, *Stuhlmann* s.n. (holo. B).

Habitat: forest and bamboo

Distribution: Kenya and Tanzania.

Notes: *C. castanostachya* is a very distinct species due to the dark red colour of its inflorescence, which is not observed in any other African *Carex* species. Verdcourt (pers. com.) states that it might have to be sunk into *C. filicina* Ness from India. On the material Schlieben 4188 in Z it is noted that the flowers are white.

***Carex chlorosaccus* C.B.Clarke**

Journ. Linn. Soc. 34: 298 (1899). *C. echinochloe* Kunze *var. chlorosaccus* (C.B.Clarke) Kük. Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 271 (1909). Syntype: Fernando Po, Clarence Peak, C. *Mann* 653 (K); Tanzania, Mt Kilimanjaro, Marango, Johnston s.n. (?).

C. leptocladus C.B.Clarke in Fl. Trop. Afr. 8: 519 (1902). Type: West Africa, Isle of St. Thomas: summit of the peak, Nov. 1861, *C. Mann* 319 (holo. K).

Habitat: Upland grassland and montane forest understory

Distribution: Kenya, Tanzania, Uganda, Malawi, DR Congo,

Notes: *C. chlorosaccus* is very similar to *C. echinochloe* but differs in 5-9 mm wide leaves, utricles 4-5.5 mm long, gradually narrowing into the 1.5-2.2 mm long glabrous or scabrid rostrellum, opposed to leaves 3-5 mm wide, utricles 3.5-4 mm long, rostrellum with fine hairs, leaf base brown or reddish.
Clarke cites in the protologue of *C. chlorosaccus* two collections: *Johnston* s.n. from Tanzania and *Mann* 653 from Fernando Po. Verdcourt (pers. com.) prefers the West African material as the type. However, the material from West African is more similar to the East African *C. echinochloe* than to the East African material of *C. chlorosaccus* which is probably a distinct species and might have to be renamed.

Carex echinochloe* Kunze subsp. *echinochloe

in C. Schkuhr, Beschr. Riedgräs., Suppl.: 47. t. 12. (1841). Type: Ethiopia, Tigre, upper Scholoda region, in stony areas *W. Schimper* 26 (holo. LZ; iso. K,P, M).

Habitat: Edge of lakes, streams and forest understory.

Distribution: Ethiopia, Kenya, Uganda and Northern Tanzania, DR Congo, Rwanda, Burundi, Sudan, Cameroon, Nigeria

Note: *C. echinochloe* is very similar to *C. chlorosaccus. C. echinochloe* differs in the usually slightly longer 5-7 mm long utricles, which very narrow very gradually into the 1.5-2.2 mm long and slender rostrellum, opposed to slightly shorter 5-6 mm long utricles, which narrow more or less gradually into the 1-1.5 mm long rostrellum in *C. chlorosaccus.*

subsp. *echinochloe*

Habitat: Edge of lakes, streams and forest understory.

Distribution: Ethiopia, Kenya, Uganda and Northern Tanzania, DR Congo, Rwanda, Burundi, Sudan, Cameroon, Nigeria

subsp. *nyasensis* (C.B.Clarke) Lye

Nordic J. Bot. 3(2): 244 (1983). *C. nyasensis* C.B.Clarke in Fl. Trop. Afr. 8: 519 (1902). C. *echinochloe* var. *nyasensis* (C.B.Clarke) Kük. Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20: 271 (1909). Type: Malawi, Masuku Plateau, *F. Whyte* s.n. (lecto. K).

Habitat: at the edge of woodland and other shady places, 1000-2250 m

Note: Lectotype was assigned by Nelmes in Kew Bull. (1940: 162) because four collections were cited at the initial species description. Distinguished from subsp. *echinochloe* by the slightly longer and less scabrid utricle. The colour difference reported by Haines and Lye (1983) is not consistent.

***Carex humpatensis* Hess**

Ber. Schweiz. Bot. Ges.: 353 (1953). Type: Angola, Chelagebirge, district Sà da Bandeira, between Tchivinguiro and Chela, in a deep gorge on horizontal Silurischen Kalksedimenten, 3 May 1952, *Hess* 52/1706, (holo. Z-Hess collection).

Habitat: in dry places, under overhanging rocks

Distribution: Angola, Chelagebirge

Note: Hess does not give any characters that would distinguish *C. humpatensis* from *C. spicato-paniculata, C. brassii*, *C. tricholepis* or *C. chlorosaccus* and its status should be more carefully investigated.

***Carex macrophyllidion* Nelmes**

Bull. Misc. Inform. Kew: 161 (1940). Type: Angola, District of Moxico, by Mfumbu in Brachystegia woodland, 7 Jan. 1938, *E.W.B.H. Milne-Redhead* 3971 (holo. K).

Habitat: shade in open forest or open bushland, 1650-2760 m.

Distribution: Tanzania, Zambia. Zimbabwe, Angola

Notes: Nelmes in Kew Bull. (1940) 161; Podlech in Mitt. Bot. Staatssamml. (1961) 121

***Carex merxmuelleri* Podlech**

Mitt. Bot. Staatssamml. M.: 121 (1961). Type: South Africa, Transvaal, Drakensberg Mts., Mariepskop, forest around the Forsthaus, ca. 1800 m, 4. Dec 1957, *Merxmüller* 553 (holo. M; iso. PRE).

Habitat: forest understory

Distribution: South Africa

Notes: This species is rarely collected and requires careful further investigation. It was not mentioned in the Flora of Natal (Gordon-Gray 1995).

***Carex neo-chevalieri* Kük. ex A.Chev.**

Bull. Mus. Hist. Nat. Paris, ser. 2, 3: 467 (1931). Type: Mali, Shere Hills, 1400 m, 18. Nov. 1930, *Hall* 2261 (P).

Habitat: Wet places at high altitude

Distribution: widespread in West Tropical Africa

Note: *C. neo-chevalieri* is somewhat similar to *C. echinochloe*, but with a less-branched inflorescence.

***Carex schliebenii* Podl.**

Mitt. Bot. Staatssamml. M.: 123 (1961). Type: Tanzania, Lumpembe, upper Ruhudje, north of the river, 1931, *H. J. Schlieben* 598 (holo. M; iso. Z).

Habitat: forest

Distribution: Southern Tanzania

Note: *C. schliebenii* is according to Podlech easily recognised by the narrow, rolled, rough, whitish-grey-green leaves. He states in the protolog that the utricles are 4 mm long. However, the type material has utricles which are 5 mm long, with a distinct, 2 mm long, rostrellum, teeth very prominent, 0.5-0.7 mm long, slightly scabrid at the edges.

***Carex spicato-paniculata* Boeckeler ex C.B.Clarke**

Fl. Cap. 7: 304 (1898). Type: South Africa, *Medley-Wood* 1190 (lecto K; isolecto. NH, BM).

Habitat: Damp places between boulder in the shade or half-shade

Distribution: Eastern and Southern Africa, Leshoto

Notes: Closely related to *C. tricholepis* Nelmes. Identifications on herbarium specimens suggest that it is often confused with *C. zuluensis*, which favours the same general habitats, and with *Schoenoxiphium rufum* and the similar species, *S. ludwigii*.

A number of specimens have smaller leaves and are annoted as a new variation (e.g. *Rogers* 18683 (PRE) or *Rehmann* 5627, which is marked as C. *spicato-paniculata* var. *viridis* (protologue not found) (PRE)). The utricle of these specimens is slightly inflated, 4 mm long, tip covered in a few scabrid hairs, suddenly narrowed into the 1.5 mm long rostrellum, teeth 1-1.5 mm long (as long as the rostrellum), leaves 4 mm wide. This is in contrast to usual material of *C. spicato-paniculata* which has not inflated, 5 mm long utricles, with a row of scabrid hairs at the edges, suddenly narrowed into the 1.5 mm long rostrellum, teeth 0.2-0.5 mm long, leaves 6-9 mm wide, fruits dense.

***Carex steudneri* Boeckeler**

Linnaea 40: 364 (1876). Type: Ethiopia, Steudner 931 (holo. K).

C. wahlenbergiana Boott var. δ *schimperi* Boott Ill. Carex 2: 101 (1860). Type: Ethiopia, Kolla, 12 Sept. 1852, *W. Schimper* 545 (P).

Habitat: grassland, bushland, rocky places, 2320-3050 m

Distribution: Ethiopia, Kenya (Cherangani Hills), Southern Tanzania, Malawi, Zimbabwe

Note: Verdcourt states, correctly, that the material currently identified as *C. steudneri* probably represents two species. Furthermore, he suggests that *C. zuluensis* should be included into *C. steudneri*. However, the absence of an inflated prophyll and evidence from DNA sequence data (Gehrke and Linder, chapter 1) show *C. zuluensis* is more closely related to *Schoenoxiphium*.

***Carex tricholepis* Nelmes**

Bull. Misc. Inform. Kew: 160 (1940). Type: Northern Rhodesia, Mwinilunga District; just south of Matonchi Farm in Brachystegia woodland, 18 Feb 1938, *E.W.B.H. Milne-Redhead* 3686A (K).

Habitat: in Brachystegia woodland

Distribution: Zimbabwe, Malawi

Note: *C. tricholepis* is similar to *C. angolensis* (see notes under *C. angolensis*).

Key for *Carex* subgenus *Indocarex* from Madagascar:

1. Utricles more than 3.5 mm long ..... 2.
1* Utricles 2.5-3.5 mm long ..... 15.

2. Utricles slightly inflated, more or less gradually narrowing towards the base, with a short rostrellum ..... 3.
2* Utricles not inflated, abruptly narrowing at the base, rostrellum more or less long ..... 4.

3. Spikelets pyramidal, dense, much branched, pistillate scales brown, leaves 5-7 mm wide ..... *C. pyramidalis*
3* Spikelets oval, little branched, pistillate scales light coloured, leaves 2-4 mm wide ..... *C. elatior*

4. Pistillate scales white with a green middle nerve ..... 5.
4* Pistillate scales more or less coloured ..... 6.

5. Leaves 1.5-2 mm wide, spikelets 1.5-2 mm long, scales erect, rostrellum one third of the length of the utricle ..... *C. graminifolia*
5* Leaves 4 mm wide, spikelets 2-4 mm long, pyramidal, scales not erect, rostrellum half the length of the utricle ..... *C. albo-viridis*

6. Utricles more than 4.5 mm long ..... 7.
6* Utricles 3-4.5 mm long ..... 13.

7. Spiklets erect or oblique (sub sessile) ..... 8.
7* Spiklets in a right angle or curved back ..... 11.

8. Utricles 6-7 mm long, rostrellum more than 2 mm long ..... 9.
8* Utricles 4.5-5.5 mm long, rostrellum less than 2 mm long ..... 10.

9. Spiklets 1-4 mm long, oval or elliptic, with a smooth peduncle, spikes crowded,utricles covered with fine hairs ..... *C. rutenbergiana*
9* Spikelets 5-6 mm long, oblong, with a scabrid peduncle, terminal spikelets widely spaced, utricles glabrous ..... *C. scabripes*

10. Leaves 4-8 mm wide, spikelets 8-10 mm long, forming dense dark head-like panicles utricles glabrous, with fine nerves ..... *C. andringitrensis*
10* Leaves 3-4 mm wide, spikelets 10-15 mm long, forming less dense panicles utricles with fine hairs, with distinct nerves ..... *C. proxima*

11. Leaves 2.5-6(-8) mm wide, utricles 6 mm long ..... *C. hirtigluma* s.l.
11* Leaves 1.5-2 mm wide, utricles 5-5.5 mm long ..... *C. hildebrandtiana*

12. Pistillate scales with fine hairs, utricles glabrous ..... *C. hirtigluma* var. *hirtigluma*
12* Pistillate scales glabrous, utricles with fine hairs ..... *C. hirtigluma* var. *arcuata*

13. Inflorescence partially head-like, not branched, panicles erect ..... *C. tsaratananensis*
13* Inflorescence never head-like, more or less branched at the base, panicles oblique or open ..... 14.

14. Leaves, 10-12 mm wide, pistillate scales with fine hairs, utricles 3.5-4.5 mm long, glabrous but distinctly nerved ..... *C. haematosacca*
14* Leaves (2-)3-8 mm wide, pistillate scales glabrous, utricles indistinct nerved ..... *C. renschiana*

15. Inflorescence only around the terminal end of the culm, utricles abruptly narrowing into the rostrellum ..... 16.
15* Inflorescence spreading far down along the culm, utricles gradually narrowing into the rostrellum ..... 17.

16. Inflorescence partially sub-pyramidal, utricles glabrous ..... *C. manongarivensis*
16* Inflorescence partially oblong, utricles with fine or scabrid hairs ..... *C. valbrayi*

17. Leaves 2-4 mm wide, pistillate scales glabrous, utricles glabrous ..... *C. bathiei*
17* Leaves 6-8 mm wide, pistillate scales loosely rough, utricles scabrid at the tip ..... *C. sambiranensis*

Carex albo-viridis C.B.Clarke

Journ. Linn. Soc. XXIX: 62 (1891). Type: Madagascar, Fort Dauphin, dry sand dunes, April 1890, *G.F. Scott Elliot* 2534 (P).

Habitat: sand dunes, 0-10 m

Distribution: South Madagascar

Note: Clarke noted on the type sheet that *C. albo-viridis* is similar to *C. hildebrandtiana*. It is similar to *C. graminifolia* with narrower leaves (1.5-2 mm wide in *Carex albo-viridis* versus 2-4 mm wide in *C. graminifolia*). It is also similar to *C. bathiei*, differing in the length of the utricles (4.5 mm as opposed to 3 mm in *C. bathiei*).

***Carex andringitrensis* Cherm.**

Bull. Soc. Bot. France 70: 410 (1923) Syntypes: Madagascar, Andringitra Mts.. Feb. 1922, *H. Perrier de la Bâthie* 14556 (syn. P). Madagascar, Andringitra Mts., Feb. 1922, *H. Perrier de la Bâthie* 14429 (syn. P).

Habitat: Rocky outcrops in grassland, 2000-2600

Distribution: Madagascar (Andringitra Mts.)

Notes: *C. andringitrensis* shares distinctive head like panicles with the similar species *C. tsaratananensis* and *C. rutenbergiana.* These species differ according to the length of the utricles: *C. andringitrensis*: 5.5 mm; *C. rutenbergiana* 6-7 mm; *C. scabripes:* 6-7 mm and *C. tsaratananensis* 3.5-4.5 mm.

***Carex bathiei* H.Lév.**

Bull. Acad. Int. Géogr. Bot. 27: 5 (1917). Type: Madagascar, Centre: Analalava, Tsitondraina Mts., sources of the Andranomalaza, Oct. 1908, *H. Perrier de la Bâthie* 2615 (holo. P).

Habitat: between rocks near streams, 1000 m

Distribution: Madagascar

Notes: *C. bathiei* is similar to *C. albo-viridis* which has longer utricles (4.5 mm, as opposed to 3 mm in *C. bathiei*) and to *C. sambiranensis* which has broader leaves (6-8 mm wide as opposed to 2-4 mm in *C. bathiei*).

***Carex elatior* Boeckeler**

Abh. Naturwiss. Vereine Bremen 7: 41 (1880). Type: Madagascar, Antananarivo, *Rutenberg* s.n. (BREM).

Habitat: forest understory, on rocky outcrops and patches with herbs, 300-1600 m

Distribution: Madagascar

Notes: Chermezon (1923) did not see the type material but listed various other sheets from P as typical for the species.

***Carex graminifolia* Cherm.**

Bull. Soc. Bot. France 70: 409 (1923). Type: Madagascar, Centre: Manankazo north east of Ankazobé, Nov. 1913, *H. Perrier de la Bâthie* 2708 (P).

Habitat: forest, 300-1500 m

Distribution: East and Central Madagascar

Note: *C. graminifolia* is similar in appearance to *C. hirtigluma*, from which it differs in generally smaller size (e.g. *C. graminifolia* is 30-70 cm tall with 1.5-2 mm wide leaves, opposed to 30-150 cm tall with 2.5-8 mm wide leaves in *C. hirtigluma*). It differs from *C. albo-viridis* in the narrower leaves (1.5-2 mm wide, as opposed to 2-4 mm in *C. albo-viridis*). It is also similar to *C. bathiei* and *C. sambiranensis* but with longer utricles (4.5 mm long as opposed to 3 mm in *C. bathiei* and *C. sambiranensis*).

Carex *haematosacca* C.B.Clarke

J. Linn. Soc., Bot. 34: 297 (1899) [as *haematosaccus*]. *C. renschiana* var. *haematosaccus* (C.B.Clarke) Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 279 (1909). Syntype: Madagascar, *R. Baron* 1085 (syn. P). Madagascar, Ivophinsornitra, *Major* 89 (syn. P).

C. renschiana Boeckeler var. *brachystachya* Cherm. Bull. Soc. Bot. France 73: 554 (1923). Type: Madagascar, West of Tamatave, Betampona near Ambodiriana, in forest, Dec. 1925, *H. Perrier de la Bâthie* 17482 (holo. P).
C. euryphylla Cherm. Bull. Soc. Bot. France 70: 411 (1923). Syntypes: Madagascar, East: Analamazoatra forest, *H. Perrier de la Bâthie* 6337 (syn. P). Madagascar, East: Analamazoatra forest, 1912, *H. Perrier de la Bâthie* 2528 (syn. P).

Habitat: forest, rocky outcrops and wet places, 200-2000 m

Distribution: Madagascar (Central and East)

Note: C. *haematosacca* differs from *C. renschiana* by its wide, coriaceous leaves. In the protologue, the collection *C.J. Meller*, s.n. (Madagascar, between Tamatave and Antananarivo, 1862 (P)), is also cited. However, this material is quite different from *R. Baron* 1085 and should instead be included in *C. renschiana.*

***Carex hildebrandtiana* Boeckeler**

Engler Bot. Jahrb. Syst. 5: 516 (1884). Type: Madagascar, Betsiléo, in swamp, Jan. 1881, *J.M. Hildebrandt* 4014 (syn. BM, M, P).
Habitat: swamps

Distribution: Madagascar

Notes: *C. hildebrandtiana* is a small species, 25-50 cm tall with 1.5-2 mm wide leaves and open panicles of only 2 spikelets with 3-7 flowers each.

***Carex hirtigluma* C.B.Clarke**

Kew Bull., Addit. Ser. 8: 73 (1908) [as *hirtiglumis*] Syntypes: Madagascar, Central *R. Baron* 694 and 4101 (syn. K).
C. stenandra Kük. Engl. Pflanzenreich, Cyperac.-Caricoid. IV 20.: 272 (1909). Type: Madagascar, s.c., s.n. (holo. P).

Habitat: forest, wet places 1000-2400 m

Distribution: Madagascar (Central)

Notes: Chermezon did not mention *C. stenandra* Kük. (Chermezon 1937: 284). The placement of *C. stenandra* in the synonymy here is on the basis of the original description by Kükenthal.

var. *hirtigluma*

Habitat: forest, ericaceous woodland, 1000-2400 m

Distribution: Madagascar (Central)

var. *perrieri* (H.Lév.) Cherm.

Bull. Soc. Bot. France 74: 608 (1927). *C. perrieri* H.Lév. Bull. Géogr. Bot. 27: 5 (1927). Type: Madagascar, Mt. Tsaratanana, 2.000-2.500 m, Dec. 1912, *H. Perrier de la Bâthie* 7429 (holo. P).

Habitat: forest, ericaceous woodland, 1000-2400 m

Distribution: Madagascar (Central)

var. *arcuata* Cherm.

Bull. Soc. Bot. France 70: 412 (1923). Type: Madagascar, Centre: Manankazo north east of Ankazobé, Nov. 1913, *H. Perrier de la Bâthie* 2708 (holo. P).

Habitat: forest, 1500-2000

Distribution: Madagascar (Mt. Tsaratanana)

***Carex manongarivensis* Cherm.**

Bull. Soc. Bot. France 70: 412 (1923). Type: Madagascar, Manongarivo, *H. Perrier de la Bâthie* 2634 (holo. P).

Habitat: moist forest

Distribution: Madagascar

Notes: According to Chermezon (1923) similar to *C. haematosacca* but distinct by the 2 mm wide leaves (vs. 8-10 mm wide), smaller utricles (2.5 mm long vs. 3.5-4.5) which have distinct veins (vs. indistinct) and the abruptly narrowing utricle (vs. more gradually narrowing).

***Carex proxima* Cherm.**

Bull. Soc. Bot. France 70: 411 (1923). Syntypes: Madagascar, Manampatrana basin, May 1919, *H. Perrier de la Bâthie* 12600 (syn. P, K). Madagascar, Ankaranan, north of Vangaindrano, May 1919, *H. Perrier de la Bâthie* 12627 (holo. P).

Habitat: forest

Distribution: Madagascar (widespread)

Notes: *C. proxima* is similar to *C. pyramidalis*, from which it differs by 3-4mm wide leaves, utricles which are not inflated and abruptly narrowing at the base, rostrellum c. 1.5 mm long (vs. leaves 5-7mm wide, utricles slightly inflated, more or less gradually narrowing towards the base, with c. 0.5 mm long rostrellum in *C. pyramidalis).*

***Carex pyramidalis* Kük.**

Bull. Herb. Boissier, II, 4: 52 (1904). Type: Madagascar, East-Imerina, Andrangoloaka in the shade of primary forest, Nov. 1880, *J.M. Hildebrandt* 3745 (syn. P, K, Z).
C. crinigera var. *minor* Boott, Illustr. *Carex* 2: 102 t. 309 (1860).Type not given.
C. gonochorica Cherm., Bull. Soc. Bot. France 72: 618 (1925). Syntypes: Madagascar, Isalo, July 1910, *H. Perrier de la Bâthie* 2438 (syn. P). Madagascar, Isalo, Nov. 1924, *H. Perrier de la Bâthie* 16702 (syn. P).

Habitat: dry forest in the shade, places with herbs or sandy patches, amongst rocks 500-2500 m

Distribution: Comoros, East and Central Madagascar

Notes: *C. gonochorica* in P appears to be young material of *C. proxima* and is not dioecious, as reported by Kükenthal (1909) and Chermezon (1923).

***Carex renschiana* Boeckeler**

Engler Bot. Jahrb. Syst. 5: 515 (1884). Type: Madagascar, Central: Andrangolaka, Nov. 1880, *J.M. Hildebrandt* 3752 (syn. P, G).
C. renschiana Boeckeler var. *laxissima* Cherm. Bull. Soc. Bot. France 70: 412 (1923). Type: Madagascar, Manongarivo Mts., May 1909, *H. Perrier de la Bâthie* 2633 (holo. P).
C. renschiana Boeckeler var. *minor* Boeckeler Engler Bot. Jahrb. Syst. 5: 516 (1884). Type: Madagascar, Central, Andrangoloaka, Nov. 1880, *J.M. Hildebrandt* 3746 (syn. K, Z).

Habitat: forest

Distribution: Madagascar

Note: Var. *minor* is supposably distinct by the narrow, less than 2mm wide, leaves, as opposed to 1.5-2 mm in var. *renschiana*. However, while the material in Z has narrow leaves, the material of the type in K and P has leaves 3-5 mm wide and much less branched inflorescences. This range probably reflects the usual variation of the species and thus var. *minor* should be sunk. Var. *laxissima* which is supposed to be distinct by the more lax inflorescence with fewer spikelets and lighter coloured pistillate scales as well as a shorter rostrellum (Chermezon 1923: 412) has been described on very young material and is also not a distinct variation.

***Carex rutenbergiana* Boeckeler**

Abh. Naturwiss. Vereine Bremen 7: 40 (1880). Type: Madagascar, *Rutenberg* s.n. (BREM).

C. emirnensis Baker J. Bot. 21: 129 t. 238, fig.2 (1883). Type unknown.
C. rutenbergiana Boeckeler var. *glomerata* Cherm. Bull Soc. bot. Fr. 70: 410 (1923). Syntypes: Madagascar, Ankaratra Mts, Feb. 1920, *H. Perrier de la Bâthie* 13002 (P) Madagascar, Ankaratra Mts, Feb. 1920, *H. Perrier de la Bâthie* 13389 (P).

Habitat: moist places 1500-2200 m

Distribution: Madagascar (Antsirabe, Ankaratra Mts., Andringitra Mts.)

Notes: *C. rutenbergiana* is very similar to *C. andringitrensis, C. scabripes* and *C. tsaratananensis* differing in the longer utricles, 6-7 mm long, while *C. andringitrensis* has 5.5 mm long utricles and *C. tsaratananensis* 3.5-4.5 mm long utricles (see also notes under *C. scabripes).*

***Carex sambiranensis* (H.Lév.) Cherm.**
Bull. Soc. Bot. France 70: 412 (1923). *C. spicato-paniculata* C:B: Clarke var. *sambiranensis* H.Lév. Bull Géogr. Bot. 27: 5 (1917). Type: Madagascar, Manogarivo Mts., near Sambirano, Sept. 1909, *H. Perrier de la Bâthie* 2648 (holo. P).

Habitat: forest, in moist places

Distribution: Madagascar

Notes: *C. sambiranensis* is similar to *C. bathiei* but has wider, 6-8 mm wide, leaves, opposed to 2-4 mm wide leaves in *C. bathiei*.

***Carex scabripes* Cherm.**

Bull. Soc. Bot. France 70: 410 (1923). Type: Madagascar, Ankaratra Mts., Tsiafagavona, eastern flanc, forested valley, Dec. 1920, *H. Perrier de la Bâthie* 13390 (P).

Habitat: forest, rocky outcrops, 1500-2600 m

Distribution: Madagascar (Andringitra Mts., Ankaratra Mts., Ivohibe)

Notes: It is difficult to distinguish *C. scabripes* from *C. andringitrensis* which has 5.5 mm long utricles, opposed to 6-7 mm in *C. scabripes*. It similar also to *C. rutenbergiana* which has 1-4 mm long spiklets and smooth peduncles (vs. spikelets 5-6 mm long, with scabrid peduncle in *C. scabripes*), as well as *C. tsaratananensis,* which has 3.5-4.5 mm long utricles.

***Carex tsaratananensis* Cherm.**

Bull. Soc. Bot. France 72: 21 (1925). Syntypes: Madagascar, Mt Tsaratanana, April 1921, *H. Perrier de la Bâthie* 16397 (syn. P) and Madagascar, Mt. Vavara (Mandrare), *H. Humbert* 6572 (syn. P).

C. tsaratananensis var. *laevis* Cherm. Mém. Acad. Malagache 10: 46 (1931). Syntype: Madagascar, near Antsirabé, Tapia valley (Sahatsio), 1600 m, 24. Dec. 1928, *H. Humbert* 7109 (P).

Habitat: ericaceous woodland or rocky outcrops

Distribution: Madagascar

Notes: Similar to *C. andringitrensis, C. rutenbergiana* and *C. scabripes* but with 3.5-4.5 mm long utricles (5.5 mm in *C. andringitrensis* and 6-7 mm in *C. rutenbergiana* and *C. scabripes*)

***Carex valbrayi* H.Lév.**

Bull. Acad. Int. Géogr. Bot. 27: 6 (1917). Type: Madagascar, Masoala, Oct. 1912, *H. Perrier de la Bâthie* 2578 (P).
Habitat: along streams

Distribution: Madagascar (North and East)

Species of uncertain affiliation:

***Carex negrii* Chiov.**

Ann. Bot. Roma x (1912) 406. Type: Ethiopia, Gala Arussi, shady macchie in narrow valley near Soddo hill, c. 1750 m, 18 June 1909, G. *Negri* 742 (holo. FT; iso. K. ex RO).

Habitat: shady macchie and damp grassy slopes

Distribution: Northern Ethiopia, Eritrea and Somalia

Notes: Hooper (1983) argues that *C. negrii* is closely related to *C. brunnea*. However, the inflorescence structure of *C. negrii*, unlike that of *C. brunnea*, resembles more that of *Schoenoxiphium*.

***Carex heterodoxa* Cherm.**

Bull. Soc. Bot. France 70: 414 (1923). Type: Madagascar, Akaratra Mts., *H. Perrier de la Bâthie* 13340 (P).

Habitat: grassland 2000-2600 m

Distribution: Madagascar (Akaratra Mts.)

Notes: *C. heterodoxa* probably belongs to *Schoenoxiphium*, but needs further investigation.

***Carex hovarum* Cherm.**

Bull. Soc. Bot. France 70: 413 (1923). Syntypes: Madagascar, Mt. Lohavohitra, *H. Perrier de la Bâthie* 12969 (P). Madagascar, Ambohimanga, *H. Perrier de la Bâthie* 7068 (P).

Habitat: ericaceous woodland 1300-1500 m

Distribution: Madagascar

Notes: Chermezon (1923) described *C. hovarum* as belonging to sect. *Hymenochlaenae* and as similar to *C. renauldi*. However, it probably belongs to *Schoenoxiphium*, but needs further investigation.

***Carex zuluensis* C.B. Clarke**

Kew Bull. Add. Ser. 8: 74 (1908). Type: South Africa, Baziya, Tembuland, *R. Baur* 1156 (Lecto K).

C. huttoniana Kük. in H.G.A.Engler (ed.), Pflanzenr., IV, 20(38): 271 (1909). Type: South Africa, Kwa-Zulu Natal, *Hutton* 344 (type locality unknown).

Habitat: Open grassland often on steep east- and south-facing slopes, occasionally in understory.

Distribution: Eastern South Africa, Leshoto

Note: The original publications cites: *Buchanan* 149, 353 South Africa, Natal (NH) as well as *Buchanan* 150, *Wood* 7540 and *Baur* 444 and 1156. Part of the original cited material seems

to belong to *C. spicato-paniculata*, and thus a lectotype was assigned by Gordon-Gray (1995: 43).

A variety (var. *glaberrima* Kük.) is noted on collection *T.C.E. Fries, T. Norlindh, H. Weimarck* 3524 (06.Dec.1930 from Zimbabwe). It is not clear if and where this name was published. It needs further investigation, as the material appears to be distinct.

Phylogenetic results from DNA sequence data suggest that *C. zuluensis* is closely related to *Schoenoxiphium*. Morphologically, it might plausibly be assigned to the subgenus *Indocarex,* were it not for the absence of an inflated prophyll.

African *Carex* names now included in Schoenoxiphium:

C. bisexualis C.B.Clarke; Fl. Cap. 7: 302 (1898) = ***S. ecklonii*** Nees

C. bolusii C.B.Clarke; Fl. Cap. 7: 304 (1898) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke**

C. buchananii C.B.Clarke in Harvey, W.H.& auct. suc. (eds.), Fl. Cap. 7: 305 (1898), nom. illeg. = ***S. rufum*** **Nees**

C. capensis Schkuhr Beschr. Riedgräs. 2: 39 (1806) = ***S. ecklonii*** **Nees**

C. capensis Thunb. Prodr. Pl. Cap.: 14 (1794) = ***S. thunbergii*** **Nees**

C. dregeana Kunth; Enum. Pl. II: 511 (1837) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke**

C. dregeana Kunth var. α; Enum. Pl. II: 511 (1837) = **S. sparteum (Wahlenb.) C.B.Clarke**

C. dregeana Kunth var. ß; Enum. Pl. II: 511 (1837) = **S. sparteum (Wahlenb.) C.B.Clarke**

C. dregeana Kunth var. major C.B.Clarke; Enum. Pl. II: 511 (1837) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke**

C. esenbeckiana Boeckeler; Linnaea, 40: 372 (1876) = ***S. lehmanii*** **(Nees) Steud.**

C. esenbeckiana Boeckeler var. *ß elongata* Boeckeler; Linnaea, 40: 372 (1876) = ***S. lehmanii*** **(Nees) Steud.**

C. indica Schkuhr; Riedgr. i. 37 (1801) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke**

C. killickii Nelmes; Bull. Misc. Inform. Kew: 89 (1955) = ***S. filiforme*** **Kük.**

C. lanceus Baill.; Hist. Pl.: 119 (1893) = ***S. lanceum*** **Kunth.**

C. lancea (Thunb.) Baill.; Hist. Pl. 12: 341 (1894) = ***S. lanceum*** **Kunth.**

C. ramosa Eckl. ex Kunth, Enum. Pl. 2: 531 (1837) = ***S. lanceum*** **(Thunb.) Kük.**

C. rufa Baill.; Hist. Pl. CXIX: 340 (1893) non Beck. = ***S. rufum*** **Nees**

C. rufa (Nees) Baill. Hist. Pl. 12: 340 (1894), nom. illeg. = ***S. rufum*** **Nees**

C. schimperiana Boeckeler Linnaea 40: 373 (1876) = ***S. lanceum*** **(Thunb.) Kük.**

C. spartea Wahlenb., Kongl. Vetensk. Acad. Nya Handl. 1803: 149 (1803) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke partially**

C. sprengelii Boeckeler nom. illeg.; Linnaea 40: 371 (1876) = ***S. sparteum*** **(Wahlenb.) C.B.Clarke**

C. uhligii K.Schum. ex C.B.Clarke Bot. Jahrb. Syst. 38: 136 (1906) = **S. lehmannii (Nees) Kunth ex Steud.**

C. zeyheri C.B.Clarke Fl. Cap. 7: 303 (1898) = ***S. ecklonii Nees***

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Uncinia digyna Hochst. ex. Steud. = ***C. monostachya* A.Rich.**	***66***
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APPENDICES:

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Appendix 1:

Accessions of taxa used in molecular phylogenetic analyses. Taxa are given in the order of *name;* author; collection or reference; distribution; [subgenus]; trnL-trnF or matK; ITS //. Sequences produced for this study marked with asteriks. Abbreviations for reference for *Carex* (*C.*)*:* D&B=Dragon & Barrington 2004 (6x), E= Escudero et al. 2007 (26x), Fo= Ford et al. 2006 (72x), Ha= Hendrichs et al. 2004a (28x), Hb= Hendrichs et al. 2004b (30x), Hi= Hipp et al. 2006 (70x), Ro= Roalson et al. 2001 (88x), R&F=Roalson and Friar 2004 (19x), St=Starr et al. 2004 (28x), W&S=Waterway and Starr 2004 (72x), Waterway and Starr (unpubl. 4x), Y&O= Yen and Olmstead 2000 (18x); References for *Ranunculus* (*R.*): Hö=Hörandl et al. 2005 (154x), Li=Ling et al. 2006 (9x), Lo=Lockhart et al. 2001 (18x), Paun et al. 2005 (95x), Xi=Xiang et al. 1997. Abbreviation for subgenera of *Carex*, which are given in square brackets are: V=*Vignea*, C=*Carex*, I=*Indocarex*; P=*Psyllophora*/*Primocarex*.

***genus*; *species;* author; collection / reference; distribution; subgenus; *trn*L-*trn*F/*mat*K; ITS//**

C. abrupta; Mack.; Hi; 4; [V]; -; AY779064 // *C. acicularis;* Boott; W&S(just NCBI) / St; 6; [P]; AY757562; AY242012 // *C. acuta;* L.; Ro; (1,2); [C]; AF284890; AF284992 // *C. acutiformis;* Ehrh.; Ro; (0,1); [C]; AF284891; AF284993 // *C. acutiformis 444;* Ehrh.; "Gehrke, Berit et al., BG-Af 444, South Africa, Eastern Cape Province, bewteen Seymour and Queenstown on R67, Melan Pass, 26 km form Seymour, 1304m, S32°23'05.2“ E26°54'41.6“ (ZH); (0,1); [C]; EU288450*; EU288567* // *C. acutiformis 459 ;* Ehrh.; "Gehrke, Berit et al., BG-Af 459, South Africa, Kwazulu Natal, between Underberg and Bushmans Nek, 1626m, S29°50'51.7“ E29°17'57.9“ (ZH); 0; [C]; EU288495*; EU288609* // *C. adusta;* Boott; Hi; 4; [V]; -; AY779065 // *C. aethiopica 465;* Schkuhr ; "Gehrke, Berit et al., BG-Af 465, South Africa, Kwazulu Natal, Cathedral Peak Area, at the fishpond, 1435m, S28°56'53.7“ E29°11'56.4“ (ZH); 0; [C]; EU288454*; - // *C. aggregata;* Mack.; Fo; 4; [V]; -; DQ115084 // *C. alata;* Torr.; Hi; 4; [V]; -; AY779066 // *C. alba ;* Scop.; Hb; (1,2); [C]; -; AY278259 // *C. albata ;* Boott ex Franch.; Fo; 2; [V]; -; DQ115086 // *C. albicans;* Willd. ex Spreng; R&F; 4; [C]; -; AY325479 // *C. albolutescens;* Schwein.; Fo; 4; [V]; -; DQ115088 // *C. albursina;* Sheldon; W&S (just NCBI); 4; [C]; AY757554; AY757626 // *C. alma;* L. H. Bailey; Ro; 4; [V]; AF284923; AF285025 // *C. alopecoidea;* Tuck.; Fo; 4; [V]; -; DQ115090 // *C. amplifolia ;* W.J. Hooker; W&S (just NCBI); 4; [C]; AY757511; AY757584 // *C. andringitrensis_264;* Cherm.; "Gehrke, Berit et al., BG-Af 264, Madagascar, massif del'Ankaratra, pic Tsiafajavona, (ZH) „ "; 0; [I]; EU288451*; EU288568* // *C. angarae;* Steud.; Ro; 4; [C]; AF284878; AF284980 // *C. angolensis_323 ;* Nelmes; "Gehrke, Berit et al., BG-Af 323, Malawi, Vipya Plateau near the elephant rock, in Miombo Woodlands, 1678m, S11°43'37.3“ E33°47'39.2“ (ZH); 0; [I]; EU288452*; EU288569* // *C. angustata;* Boott; Ro; 4; [C]; AF284913; AF285015 // *C. annectens;* (E.P. Bicknell) E. P. Bicknell,; Fo; 4; [V]; -; DQ115092 // *C. antoniensis;* A. Chev.; Ro; 5; [C]; AF284939; AF285041 // *C. appalachica;* J. M. Webber & P. Ball; W&S (just NCBI); 4; [V]; AY757490; AY757401 // *C. appressa; R.* Br.; Briggs et al. 2000 / Fo; 6; [V]; AF148726; DQ115094 // *C. appropinquata;* Schum.; Ha; 1; [V]; -; AY280549 // *C. aquatilis;* Wahlenb.; Ro; (1,2,4); [C]; AF284892; AY278301 // *C. arapahoensis ;* Clokey; Hi; 4; [V]; -; AY779068 // *C. arenaria;* L. ; Ha; (1,2); [V]; -; AY280529 // *C. argyrantha;* Tuck. ex Dewey; Hi; 4; [V]; -; AY779069 // *C. athrostachya ;* Olney; Ha; 4; [V]; -; AY280539 // *C. atlantica;* L.H. Bailey; Fo; 4; [V]; -; DQ115104 // *C. atrata;* L.; Hb; (1,2); [C]; -; AY278263 // *C. atrata subsp. atterima;* L.; "Guibert, Cyril CyG2181, Switzerland, Engadin, St Moritz N46°30'11.7“ E009°50'45.86“ (ZH); (1,2); [C]; EU288425*; EU288542* // *C. atrofusca;* Schkuhr; Schoenswetter et al. 2006 / Hb; (1,2,4); [C]; AM085581; AY278313 // *C. aurea;* Nutt.; Ro; 4; [C]; AF284960; AF285062 // *C. austro-africana 450;* (Kük.) Raymond; "Gehrke, Berit et al., BG-Af 450, South Africa, Kwazulu Natal, between Kokstad and Underberg along R617, bridge over Mzuntlava River, 1490m, S30°23'04.8“ E29°26'57.9“ (ZH); 0; [C]; EU288453*; EU288570* // *C. austroalpina;* Becherer; Hb; 1; [C]; -; AY278276 //

C. baccans; Nees in wight; Fo; 2; [C]; AF191814; - // *C. backii;* Boott; St / Fo; 4; [P]; AY757494; AF027411 // *C. baldensis;* L.; Guibert, Cyril CyG2100, Botanical Garden of the University of Zurich, (ZH); 1; [P]; EU288426*; EU288543* // *C. baronii 283; Baker* ; Gehrke, Berit et al., BG-Af 283, Madagascar, Parc National d'Andringitra, river (Riambavy) crossing beneath camp 2, 1950m (ZH); 0; [I]; EU288482*; EU288583* // *C. basiantha ;* Steud.; St; 4; [P]; AF284868; AF284970 // *C. bebbii ;* (L.H. Bailey) Fernald; Hi; 4; [V]; -; AY779071 // *C. bella;* Bailey; Ro; 4; [C]; AF284864; AF284966 // *C. bequaertii_079 ;* De Wild.; "Gehrke, Berit et al., BG-Af 079, Kenya, Mount Kenya National Park, Naro Moru Route to Mackinders Camp just at the beginning of the track, 3155m, S00°10'10.0" E37°13'03.6" (ZH); 0; [C]; EU288456*; EU288572* // *C. bequaertii_098 ;* De Wild.; "Gehrke, Berit et al., BG-Af 098, Kenya, Mount Kenya National Park, Sirimon Route path between Old Moses Camp and Shiptons Camp, 3308m, S00°02'14.5" E37°17'12.4" (ZH); 0; [C]; EU288457*; EU288573* // *C. bequaertii_145 ;* De Wild.; "Gehrke, Berit et al., BG-Af 145, Kenya, Mount Elgon National Park, Koroborte - Koitoboss track (Park Route), 3503m, N01°06'07.6" E34°43'29.2" (ZH); 0; [C]; EU288458*; EU288574* // *C. bequaertii_241 ;* De Wild.; "Gehrke, Berit et al., BG-Af 241, Ethiopia, Bale Mountains National Park, Gaysay Valley, river on the road between Dodola and Dinsho, 2892m, N07°06'36.3" E39°45'43.1" (ZH); 0; [C]; EU288459*; EU288575* // *C. bequaertii_352 ;* De Wild.; "Gehrke, Berit et al., BG-Af 352, Uganda, Rwenzori Mts., between Nyabitaba Hut and John Matte Hut, 3277m, N00°22'50.2" E29°56'32.5" (ZH); 0; [C]; -; EU288576* // *C. bequaertii* var. *maxima 014;* De Wild.; "Gehrke, Berit et al., BG-Af 014, Kenya, Aberdares National Park, Oldonyio Lesatima, road from the fire watch tower to the peak, 3488m, S00°20'20.9" E36°39'20.7" (ZH); 0; [C]; EU288455*; EU288571* // *C. bicknellii;* Britton; Ro; 4; [V]; AF284937; AF285039 // *C. bicolor;* All.; Marazzi, Brigitte BM206, Switzerland, Zermatt 2400-2480m N46°01'53.1" E007°44'27.3" (ZH); (1,2,4); [C]; -; EU288544* // *C. bigelowii;* Torr. ex Schwein.; R&F; (1,2,4); [C]; -; AY278303 // *C. binervis;* Smith; E; 0; [C]; -; DQ384112 // *C. blanda;* Dewey; W&S (just NCBI); 4; [C]; AY757555; AF027445 // *C. bohemica;* Schreb.; Ro; (1,2); [V]; AF284887; AF284989 // *C. bolanderi;* Olney; Hi; 4; [V]; -; DQ461132 // *C. bonariensis;* Desf.; Fo; 5; [V]; -; DQ115106 // *C. bonplandii;* Kunth; Ha; (4,5); [V]; -; AY280563 // *C. brachystachys;* Schrank (& Moll); Hb; 1; [C]; -; AY278277 // *C. brainerdii ;* Mack.; R&F; 4; [C]; -; AY325485 // *C. brevicaulis;* Thou.; Ro/R&F; 4; [C]; -; AY325471 // *C. brevicollis;* DC. Ro; 1; [C]; AF284909; AF285011 // *C. brevior;* (Dewey) Mack. ex Lunell; Hi; 4; [V]; -; AY779075 // *C. breweri;* Boott; St; 4; [P]; AF284910; AF285012 // *C. brizoides;* L.; Ha; 1; [V]; -; AY280546 // *C. bromoides;* Schkuhr; W&S/ Ha; 4; [V]; AY757474; AY280534 // *C. brunnea;* Thunb.; Ro; (1,2,6); [C]; AF284901; AF285003 // *C. brunnescens;* (Pers.) Poir.; Ha; (1,2,4); [V]; AY757481; AY280567 // *C. buxbaumii;* Wahlenb.; Guibert, Cyril CyG2060, Switzerland, Alp Flix N46°32'03.20" E009°38'33.11" (ZH); (1,2,4,6); [C]; EU288426*; EU288545* // *C. camposii;* Boiss. & Reut.; E; 3; [C]; -; DQ384115 // *C. canariensis;* Kük.; Ha; 3; [V]; -; AY280558 // *C. canescens;* L.; W&S/ Ha; (1,2,4,5,6); [V]; AF284888; AF284990 // *C. capillacea;* Boott; Fo; (2,6); [P]; AF164925; - // *C. capillaris ;* L.; Guibert, Cyril CyG2052, Switzerland, Graubünden, Alp Flix 2072m N46°31'47.5" E009°39'00.3" (ZH); (1,2,4); [C]; EU288429*; EU288546* // *C. capitata;* L.; Ro; (1,2,4,5); [V]; AF284942; AF285044 // *C. capitata;* L.; St; (1,2,4,5); [P]; AF284942; AF285044 // *C. caryophyllea;* Latourr.; "Guibert, Cyril CyG9A, Switzerland, Stäfa N47°14'56" E008°43'52.5" (ZH); (1,2); [C]; EU288430*; EU288547* // *C. castanea;* Wahlenb.; Ro; 4; [C]; AF284956; AF285058 // *C. cephaloidea;* (Dewey) Dewey; W&S/ Hi; 4; [V]; AY757465; AY779080 // *C. cephalophora ;* Muhl. ex Willd.; W&S/ Fo; 4; [V]; AY757466; DQ115120 // *C. cherokeensis;* Schwein.; W&S (just NCBI); 4; [C]; AY757546; AY757619 // *C. chihuahuensis;* Mack.; Fo; 4; [V]; -; DQ115122 // *C. chlorosaccus_106;* C.B. Clarke; "Gehrke, Berit et al., BG-Af 106, Kenya, Mount Kenya National Park, Sirimon Route, small stream below the bandas, 2600m, N00°03'25.7" E37°17'21.4" (ZH); 0; [I]; EU288460*; - // *C. chlorosaccus_152;* C.B. Clarke; "Gehrke, Berit et al., BG-Af 152, Kenya, Saiwa Samp National Park, , 1811m, N01°02'17.4" E34°47'10.7" (ZH); 0; [I]; EU288461*; EU288577* // *C. chordorrhiza ;* Ehrh.; Ro / Ha;

(1,2,4); [V]; AF284990; AY280568 // *C. circinata ;* C.A: Mey.; St; 4; [P]; AF284911; AF285013 // *C. cognata_cognata_315;* Kunth; "Gehrke, Berit et al., BG-Af 315, Malawi, Nyika National Park, Zungwara road, little forest area dominated by Hagenia on the south-east slope, 2317m, S10°30'15.2“ E33°46'47.8“ (ZH); 0; [C]; EU288463*; EU288578* // *C. collinsii;* Nutt.; W&S (just NCBI); 4; [C]; AY757543; AY757616 // *C. collumanthus;* (Steyerm.) Mora; St; 5; [C]; AY241987; - // *C. communis;* Bailey; Ro; 4; [C]; AF284874; AF284976 // *C. comosa;* Boott; W&S (just NCBI); 4; [C]; AF757502; AY757575 // *C. complanata ;* Torr. & Hook.; W&S (just NCBI); (4,5); [C]; AY757531; AY757604 // *C. composita;* Boott; Fo; 2; [C]; AF191815; - // *C. concinnoides;* Mack.; Ro; 4; [C]; AF284863; AF284965 // *C. conferta var. conferta 197;* Hochst. ex A. Rich.; Berit Gehrke et al., BG-Af 197, Ethiopia, Menangesha Suba State Forest Juniperus dominated forest, 2615m, N08°58'06.8“ E38°34'00.3“ (ZH); 0; [V]; EU288464*; - // *C. conferta* var. *conferta 237;* Hochst. ex A. Rich.; Berit Gehrke et al., BG-Af 237, Ethiopia, Bale Mountains National Park Gaysay Valley, river on the road between Dodola and Dinsho, 3060m, N07°05'38.3“ E39°47'35.5“ (ZH); 0; [V]; EU288465*; EU288579* // *C. leptosaccus x lycurus 175;* ; Berit Gehrke et al., BG-Af 175, Kenya, road between Nakuru and Eldoret (A104) small water dam close to Timboroa, 2701m, N00°02'38.8“ E35°32'28.1“ (ZH); 0; [V]; EU288467*; EU288581* // *C. leptosaccus 375* Hochst. ex A. Rich. and (C.B. Cl.) Kük.; Berit Gehrke et al., BG-Af 375, Uganda, Ruwenzori Mts. between Guy Yeoman Hut and Nyabitaba Hut, 3494m, N00°20'59.7“ E29°56'15.3“ (ZH); 0; [V]; EU288466*; EU288580* // *C. lycurus 131;* Hochst. ex A. Rich. and (K. Schum) Lye; Berit Gehrke et al., BG-Af 131, Kenya, Mount Elgon National Park, 2475m, N01°03'28.7“ E34°45'49.4“ (ZH); 0; [V]; EU288468*; EU288582* // *C. lycurus 312;* Hochst. ex A. Rich. and (K. Schum) Lye; Berit Gehrke et al., BG-Af 312, Malawi, Nyika National Park road to Nganda Hill shortly before the summit, 2365m, S10°30'04.0“ E33°50'57.8“ (ZH); 0; [V]; EU288469*; EU288583* // *C. lycurus 334;* Hochst. ex A. Rich. and (K. Schum) Lye; Berit Gehrke et al., BG-Af 334, Southern, Tanzanian, Iringa District, Kitulo Plateau, wet and densely vegetated little stream on road from Mgeta, 2635m, S09°01'35.0“ E33°45'34.6“ (ZH); 0; [V]; EU288470*; EU288584* // *C. conjuncta;* Boott; Fo; 4; [V]; -; DQ115130 // *C. constanceana ;* Stacey; Hi; 4; [V]; -; AY779088 // *C. cordillerana ;* Saarela & B. A. Ford; Fo; 4; [V]; -; DQ115132 // *C. crawfordii;* Fernald; Hi; 4; [V]; -; AY779089 // *C. cretica;* Gradst. & J. Kern; E; 3; [C]; -; DQ384116 // *C. crinita;* Lam.; W&S (just NCBI); 4; [C]; AY757516; AY757589 // *C. cristatella;* Britton in Britton & A. Brown; Fo; 4; [V]; -; DQ115134 // *C. cruciata;* Wahlenb.; W&S (just NCBI); 2; [C]; AY757558; AF027450 // *C. crus-corvi;* Shuttl. in Kunze; W&S / Fo; 4; [V]; AY757469; DQ115136 // *C. cumulata;* (L.H. Bailey) Mack.; Hi; 4; [V]; -; AY779091 // *C. curaica;* Kunth; Hi; 2; [V]; -; AY779092 // *C. curvata;* Knaf; Ha; 1; [V]; -; AY280530 // *C. curvula;* All.; W&S/ St; 1; [P]; AY757564; AY242030 // *C. curvula subsp. rosae;* Gilomen; "Marazzi, Brigitte BM210, Switzerland, Graubünden, Alp Flix 2386m N46°31'12.1“ E09°40'09.7“ (ZH); 1; [P]; EU288431*; - // *C. cusickii;* Mack. ex Piper & Beattie; Fo; 4; [V]; -; DQ115138 // *C. davalliana;* Smith; "Linder, Peter PL7869, Switzerland, Zürich, Sihlwald 680m N47°16'07.6“ E008°32'26.5“ (ZH); 1; [V]; EU288432*; EU288548* // *C. davyi;* Mack.; Hi; 4; [V]; -; AY779093 // *C. debilis;* Michx.; Ro; (1,4); [C]; AF284927; AF285029 // *C. decomposita;* Muhl.; W&S/ Fo; 4; [V]; AY757472; DQ115140 // *C. deflexa var. deflexa;* Hornem.; R&F; 4; [C]; -; AY686720 // *C. demissa;* Hornem.; Hb; (1,2,3); [C]; -; AY278307 // *C. demissa_D;* Hornem.; E; (1,2,3); [C]; -; AY278307 // *C. densa;* L.H. Bailey; Ha; 4; [V]; -; AY280538 // *C. depauperata;* Curt. ex With.; W&S (just NCBI)/St; (1,2); [C]; AY757549; AY241984 // *C. deweyana;* Schw.; W&S/ St; (2,4); [V]; AY757475; AF027437 // *C. diandra;* Schrank; Ro; (2,4,6); [V]; AF284924; AF285026 // *C. digitalis;* Willd.; Ro; 4; [C]; AF284933; AF285035 // *C. digitata;* L.; Ro; 1; [C]; AF284902; AF285004 // *C. diluta;* M. Bieb.; E; (1,2,3); [C]; -; DQ384120 // *C. dioica ;* L.; Fo / Ha; (1,2); [V]; AF191816; AY280543 // *C. disperma;* Dewey; W&S/ Fo; (1,2,4); [V]; AY757489; DQ115148 // *C. distans;* L.; Hb; (1,2,3); [C]; -; AY278312 // *C. disticha;* Lam.; Guibert, Cyril CyG2156, Botanical Garden Bonn (ZH); (1,2,6); [V]; EU288433*; EU288549* // *C. divisa ;* Huds.; Ro / Ha; (1,2); [V]; AF284916; AY280552 // *C. divulsa;* Stokes; Ha; (1,2,3); [V]; -; AY280553

// *C. donnell-smithii;* Bailey; Ro; 4; [C]; AF284903; AF285005 // *C. douglasii;* Boott; Fo; 4; [V]; -; DQ115156 // *C. drakensbergensis 481 ;* C.B.Clarke; "Gehrke, Berit et al., BG-Af 481, South Africa, Kwazulu Natal, Golden Gate National Park, second loup, at the beginning of the loup near stream crossing, 1947m, S28°30'43.0" E28°38'21.2" (ZH); 0; [C]; -; - // *C. duriuscula;* C.A. Mey.; Ro; (1,2,4,6); [V]; -; AF027436 // *C. ebenea ;* Rydb.; Hi; 4; [V]; -; AY779095 // *C. eburnea;* Boott; Ro; 4; [C]; AF284898; AF285000 // *C. echinata;* Murray; W&S/ Ha; (1,2,4,6); [V]; AY757477; AY280559 // *C. echinochloe_161;* Kunze; "Gehrke, Berit et al., BG-Af 161, Kenya, Saiwa Swamp National Park,1893m, N01°11'53.3" E35°12'85.4" (ZH); 0; [I]; EU288471*; EU288585* // *C. echinochloe_nyassensis_339;* (C.B.Clarke) Lye; "Gehrke, Berit et al., BG-Af 339, Southern Tanzania, Morogoro District, Uluguru Mountains, path to Lukwangule Plateau, path from Nyandira, 1870m, S07°06'29.9" E37°35'89.3" (ZH); 0; [I]; EU288472*; EU288586* // *C. egglestonii;* Mack.; Hi; 4; [V]; -; AY779097 // *C. elata;* All.; Hb; (1,2); [C]; -; AY278255 // *C. elongata;* L.; Ha; 1; [V]; -; AY280560 // *C. elynoides ;* T. Holm.; Fo; 4; [P]; AF164926; - // *C. ericetorum ;* Pollich; Ro; (1,2); [C]; AF284872; AF284974 // *C. erythrorrhiza 238;* Böck.; Berit Gehrke et al., BG-Af 238, Ethiopia, Bale Mountains National Park Gaysay Valley, river on the road between Dodola and Dinsho, 3060m, N07°05'38.3" E39°47'35.5" (ZH); 0; [V]; EU288476*; EU288590* // *C. erythrorrhiza 245;* Böck.; Berit Gehrke et al., BG-Af 245, Ethiopia, Road from Dodola to Addis via Asala smaller river ca. 1300 m; 0; [V]; EU288477*; EU288591* // *C. exilis ;* Dewey; W&S/ Fo; 4; [V]; AY757478; DQ115168 // *C. exsiccata;* Bailey; Ro; 4; [C]; AF284953; AF285055 // *C. extensa;* Good.; Hb; (1,3); [C]; -; AY278311 // *C. falcata;* Turcz.; Ro; 2; [C]; AF284914; AF285016 // *C. fecunda;* Steud.; Fo (just NCBI); 5; [C]; -; DQ115170 // *C. fecunda;* Steud.; Fo; 5; [V]; -; DQ11517 // *C. ferruginea ;* Scop.; Linder, Peter PL7647, Switzerland, Bluemlisalp 2026m N46°30'98.4" E007°46'16.6" (ZH); (1,3); [C]; EU288434*; EU288550* // *C. festucacea;* Schkuhr ex Willdenow; Hi; 4; [V]; -; AY779098 // *C. feta;* L.H. Bailey; Hi; 4; [V]; -; AY779099 // *C. filicina;* Nees; Ro; 2; [I]; AF284879; AF284981 // *C. fimbriata;* Schkuhr; "Guibert, Cyril CyG2185, Switzerland, Engadin, Pontresina 2059m N46°26'09.4" E09°59'28.7" (ZH); 1; [C]; EU288435*; EU288551* // *C. fissirostris;* Ball; E; 3; [C]; -; DQ384132 // *C. fissuricola;* Mack.; W&S (just NCBI); 4; [C]; AY757544; AY757617 // *C. flacca;* Schreb.; Hb; (1,2); [C]; -; AY278274 // *C. flacca subsp. serrulata;* Schreb. / (Biv.) Greuter; Ro; (1,2); [C]; AF284880; AF284982 // *C. flava;* L.; Ro; (1,2,4); [C]; AF284905; AF28500 // *C. floridana;* Schw.; R&F; 4; [C]; -; AY325482 // *C. foenea ;* Willd.; Hi; 4; [V]; -; AY779100 // *C. foetida;* All.; Ha; 1; [V]; -; AY280544 // *C. folliculata;* L.; W&S (just NCBI); 4; [C]; AY757528; AY757601 // *C. fracta ;* Mack.; Ro; 4; [V]; AF284928; AF285030 // *C. frigida;* All.; Hb; 1; [C]; -; AY278291 // *C. fuliginosa ;* Schkuhr; Hb; (1,2,4); [C]; -; AY278254 // *C. fuscula subsp. fuscula;* d'Urv; E; 5; [C]; -; DQ384138 // *C. gaudichaudiana ;* Kunth; D&B; 6; [C]; -; AY770472 // *C. geophila;* Mack.; R&F; (4,5); [C]; -; AY325474 // *C. gibba;* Wahlenb.; Fo; 2; [V]; -; DQ115174 // *C. gigas;* (Holm) Mack.; Ro; 4; [C]; AF284925; AF285027 // *C. glacialis;* Mack.; W&S (just NCBI); (1,2,4); [C]; AY757553; AY757625 // *C. globosa;* Boott; R&F; 4; [C]; -; AY325487 // *C. globularis ;* L.; Ro; (1,2); [C]; AF284947; AF285049 // *C. glomerabilis 425 ;* Krecz.; Berit Gehrke et al., BG-Af 425, South Africa, Western Cape Province east of Barrydale on R62, 499m, S33°51'21.0" E20°50'09.9" (ZH); 0; [V]; EU288478*; EU288593* // *C. glomerabilis 431 ;* Krecz.; Berit Gehrke et al., BG-Af 431, South Africa, Western Cape Province small road between Wilderness and Sedgefield near railway tracks; 0; [V]; EU288479*; EU288594* // *C. gracilior;* Mack.; Hi; 4; [V]; -; AY779102 // *C. gracillima ;* Schwein.; Ro; 4; [C]; AF284952; AF285054 // *C. graminifolia_296;* Cherm.; "Gehrke, Berit et al., BG-Af 296, Madagascar, Parc National d'Andringitra, circuit Imaitso , 1600m, S22°09'01.7" E46°56'55.9" (ZH); 0; [I]; EU288480*; EU288596* // *C. gravida c.f.;* L.H. Bailey; Hi (only NCBI); 4; [V]; -; AY779083 // *C. grayi;* Carey; W&S (just NCBI); 4; [C]; AY757507; AY757580 // *C. grioletii;* Roemer; Ro; (1,3); [C]; AF284946; AF285048 // *C. gunniana;* Boott; E; 6; [C]; -; DQ384145 // *C. gynocrates;* Wormsk. ex Drejer; Fo; (2,4); [V]; AY757479; DQ115176 // *C. hakkodensis;* Franch.; Fo; 2; [P]; AF164936; - // *C. harfordii;* Mack.; Hi; 4; [V]; -; AY779104 // *C. hartmanii;* Cojander; Guibert, Cyril

CyG2187, Botanical Garden of the University of Zurich, (ZH); (1,2); [C]; EU288436*; EU288552* // *C. haydeniana;* Olney; Hi; 4; [V]; -; AY779105 // *C. haydenii;* Dewey; Hi; 4; [C]; -; AY779106 // *C. heleonastes;* Ehrh.; W&S/ Ha; (1,2,4); [V]; AY757484; AY280566 // *C. helodes;* Link; E; (1,3); [C]; -; DQ384147 // *C. hermannii;* Cochrane; D&B; 4; [C]; -; AY770473 // *C. hirta;* L.; "Guibert, Cyril CyG2132 ZH, Switzerland, Chausen 648m N47°14'33.9“ E008°35'49.4“ (ZH); (1,2); [C]; EU288437*; EU288553* // *C. hirtifolia ;* Mack.; W&S (just NCBI); 4; [C]; AY757538; AY757611 // *C. hirtiglumis_var_arcuata_295; C.* B. Clarke var. Cherm.; "Gehrke, Berit et al., BG-Af 295, Madagascar, Parc National d'Andringitra, circuit Imaitso , 1548m, S22°09'01.7“ E46°56'55.9“ (ZH); 0; [I]; -; EU288595* // *C. hirtiglumis_var_arcuata_300; C.* B. Clarke var. Cherm.; "Gehrke, Berit et al., BG-Af 300, Madagascar, Ivohibe, western slope of the moutain, 1400m, S22°29'44“ E46°57'01“ (ZH) "; 0; [I]; EU288481*; EU288596* // *C. hispida;* Willd. ex Schkuhr; Hendrichs, Matthias MH2947 see also AY278272 (ITS); 3; [C]; EU288438*; EU288554* // *C. hitchcockiana;* Dewey; W&S (just NCBI); 4; [C]; AY757541; AY757614 // *C. hoodii ;* Boott; Fo; 4; [V]; -; DQ115178 // *C. hookerana;* Dewey; Fo; 4; [V]; -; DQ115180 // *C. hormathodes;* Fernald; Fo; 4; [V]; -; DQ115182 // *C. hostiana;* DC. "Guibert, Cyril CyG2062, Switzerland, Alp Flix N46°32'03.20“ E009°38'33.11“ (ZH); (1,4); [C]; EU288439*; EU288555* // *C. humboldtiana;* Steud.; Fo; 5; [C]; AF191819; - // *C. humilis;* Leysser; Ro; (1,2); [C]; AF284906; AF285008 // *C. hyalina;* Boott; Hi; 4; [V]; -; AY779109 // *C. hystericina;* Muhl. ex Wild.; W&S (just NCBI); 4; [C]; AY757501; AY757574 // *C. idaea;* Greuter et al.; E; 3; [C]; -; DQ384153 // *C. illota ;* L.H. Bailey; Fo; 4; [V]; -; DQ115184 // *C. incurviformis;* Mack.; Fo; 4; [V]; -; DQ115186 // *C. inops subsp.heliophila;* ; R&F; 4; [C]; -; AY325484 // *C. inops subsp.inops;* .Bailey; R&F; 4; [C]; -; AY686721 // *C. integra;* Mack.; Hi; 4; [V]; -; AY779111 // *C. interior;* L.H. Bailey; W&S/ Fo; 4; [V]; AY757476; DQ115188 // *C. interjecta;* Reznicek; W&S/ Hi; 4; [V]; AY757476; AY779113 // *C. intumescens;* Rudga; W&S (just NCBI); 4; [C]; AY757506; AY757579 // *C. inversa; R.* Br.; Fo; 6; [V]; -; DQ115190 // *C. johnstonii_195 ;* Boeck.; "Gehrke, Berit et al., BG-Af 195, Ethiopia, Menangesha Suba State Forest, *Juniperus* dominated forest, 2615m, N08°58'06.8“ E38°34'00.3“ (ZH); 0; [C]; EU288483*; EU288598* // *C. johnstonii_340;* Boeck.; "Gehrke, Berit et al., BG-Af 340, Southern Tanzania, Morogoro District, Uluguru Mountains, path to Lukwangule Plateau from Nyandira, 2432m, S07°06'89.3“ E37°36'61.1“ (ZH); 0; [C]; -; EU288599* // *C. johnstonii_377 ;* Boeck.; "Gehrke, Berit et al., BG-Af 377, Uganda, Ruwenzori Mts., between Guy Yeoman Hut and Nyabitaba Hut , 2818m, N00°21'12.8“ E29°58'06.0“ (ZH); 0; [C]; -; EU288600* // *C. jonesii;* L. H. Bailey; W&S/ Ro; 4; [V]; AF284936; AF285038 // *C. kitaibeliana;* Degen ex Becherer; Ro; 1; [C]; -; AY278258 // *C. kobomugi;* Ohwi; Fo; 2; [V]; -; DQ115194 // *C. lachenalii;* Schkuhr; "Guibert, Cyril CyG2073, Switzerland, Graubünden, Alp Flix 2454m N46°31'00.5“ E009°40'59.3“ (ZH); (1,2,4,6); [V]; EU288440*; EU288556* // *C. laeviculmis;* Meinsh.; Fo; 4; [V]; -; DQ115196 // *C. laevigata;* Smith; E; (1,3); [C]; -; DQ384156 // *C. laevissima;* Nakai; Fo; 2; [V]; -; DQ115198 // *C. laevivaginata;* (Kük.) Mack. in Britton & A. Brown; W&S/ Fo; 4; [V]; AY757470; DQ115200 // *C. lagunensis c.f.;* M.E. Jones; Hi; 4; [V]; -; AY779084 // *C. lainzii;* Luceno,Rico & Romero; E; (1,3); [C]; -; DQ384161 // *C. lanceolata ;* Boott; Ro; 2; [C]; AF284907; AF285009 // *C. lanuginosa ;* Michx.; Ro; 4; [C]; AF284929; AF285031 // *C. lasiocarpa ;* Boott; Ro; (1,2,4); [C]; -; AY278297 // *C. laxiflora;* Lam.; Hb; 4; [C]; AF284862; AF284964 // *C. leavenworthii;* Dewey; Ro; 4; [V]; AF284931; AF285033 // *C. leersii;* F.W. Schultz; Ha; (1,2); [V]; -; AY280554 // *C. lemmonii;* Boott; Hb; 4; [C]; AF284869; AF284971 // *C. lenticularis;* Michx.; D&B; 4; [C]; -; AY770477 // *C. lepidocarpa;* Tausch; Ro; 1; [C]; -; AY278293 // *C. lepidocarpa_D;* L.; E; (1,2,3); [C]; -; DQ384164 // *C. leporinella;* Mack.; Hi; 4; [V]; -; AY779114 // *C. leptalea;* Wahlenb.; Ro; 4; [P]; AF284958; AF285060 // *C. leucodonta ;* Holm; Ro; 4; [C]; AF284871; AF284973 // *C. ligerica;* Gay; Guibert, Cyril CyG_BotGarden001, Botanical Garden of the University of Zurich, (ZH); (1,2); [V]; EU288441*; EU288557* // *C. limosa;* L.; Ro; (1,2,4); [C]; AF284899; AY278298 // *C. liparocarpos;* Gaudin; Ro; (1,3); [C]; -; AY278261 // *C. livida;* (Wahlenb.) Willd.; W&S (just NCBI); (1,2,4); [C]; AY757556; AY757628 // *C. loliacea;* L.; Fo; (1,2,4); [V]; -; DQ115206 // *C. longii ;*

Mack.; Hi; (4,5); [V]; -; AY779115 // *C. longipedunculata_027;* K. Schum.; "Gehrke, Berit et al., BG-Af 027, Kenya, Aberdares National Park, road to Fishing Bandas, 2928m, S00°20'31.2“ E36°47'52.9“ (ZH); 0; [C]; EU288484*; EU288601* // *C. longipedunculata_311;* K. Schum.; "Gehrke, Berit et al., BG-Af 311, Malawi, Nyika National Park, road to Nganda Hill shortly before the summit, 2365m, S10°30'04.0“ E33°50'57.8“ (ZH); 0; [C]; EU288485*; - // *C. longipedunculata_091;-* ; "Gehrke, Berit et al., BG-Af 091, Kenya, Mount Kenya National Park, Sirimon Route, close to the Sirimon Bandas by Park Gate, 2585m, S00°00'21.9“ E37°14'54.2“ (ZH); 0; [C]; -; EU288630* // *C. longipedunculata_092;-* ; "Gehrke, Berit et al., BG-Af 092, Kenya, Mount Kenya National Park, Sirimon Route, close to the Sirimon Bandas by Park Gate, 2585m, S00°00'21.9“ E37°14'54.2“ (ZH); 0; [C]; -; EU288631* // *C. lowei;* Becherer; E; 3; [C]; -; DQ384166 // *C. lucorum;* Willd. ex Link; R&F; 4; [C]; -; AY325464 // *C. lugens;* T. Holm; Gielly et al. 2006; (2,4); [C]; DQ860537; - // *C. lupulina;* Muehlenb. ex Willd.; Hb; 4; [C]; AF284861; AF284963 // *C. lurida;* Wahlenb.; R0; (4,5); [C]; AF284860; AF284962 // *C. luzulifolia;* Boott; W&S (just NCBI); 4; [C]; AY757545; AY757618 // *C. luzulina;* Olney; Hb; 4; [C]; -; AY278252 // *C. maackii;* Maximovicz.; Hi; (0,1,2,4,5); [V]; -; AY779116 // *C. mackenziei;* V. I. Krecz. in Kom. et al.; F0; (1,2,4); [V]; -; DQ115208 // *C. macloviana;* d'Urv.; Ha; (1,2,4,5); [V]; -; AY280562 // *C. macrocephala ;* Willd.; R0; 2; [V]; AF284915; AF285017 // *C. macrorrhiza;* Boeck.; R0; 5; [V]; AF284916; AF285018 // *C. madagascariensis_289;* Boeck.; Gehrke, Berit et al., BG-Af 289, Madagascar, Parc National d'Andringitra, river (Riambavy) crossing beneath camp 2, 1950m (ZH); 0; [C]; EU288486*; EU288602* // *C. magellanica;* Lam.; W&S (just NCBI); (1,2,4,5); [C]; AY757521; AY757594 // *C. mairii;* Cosson & Germ.; Hb; 3; [C]; -; AY278253 // *C. mandshurica;* Meinsh.; R0; (1,3); [C]; AF284943; AY325432 // *C. mannii;* Becherer; E; 0; [C]; -; DQ384171 // *C. mannii_010 ;* E.A.Bruce; "Gehrke, Berit et al., BG-Af 010, Kenya, Aberdares National Park, Oldonyio Lesatima, road from the fire watch tower to the peak, 3488m, S00°20'20.9“ E36°39'20.7“ (ZH); 0; [C]; EU288488*; EU288603* // *C. mannii_029 ;* E.A.Bruce; "Gehrke, Berit et al., BG-Af 029, Kenya, Aberdares National Park, road to Fishing Bandas, 3066m, S00°24'42.9“ E36°43'26.5“ (ZH); 0; [C]; EU288489*; EU288604* // *C. marianensis;* Stacey; F0; 4; [V]; -; DQ115212 // *C. mariposana;* L.H. Bailey; Hi; 4; [V]; -; AY779118 // *C. maritima;* Gunn.; W&S/ F0; (1,2,4,5); [V]; AY757493; DQ115214 // *C. mendocinensis;* Olney ex Boott in S.Watson & al.; W&S (just NCBI); 4; [C]; AY757536; AY757609 // *C. merritt-fernaldii;* Mack.; Hi; 4; [V]; -; AY779119 // *C. mertensii;* Prescott; W&S (just NCBI); (2,4,5); [C]; AY757519; AY757592 // *C. mesochorea;* Mack.; F0; 4; [V]; -; DQ115216 // *C. michauxiana;* Boeck.; W&S (just NCBI); (2,4); [C]; AY757529; AY757602 // *C. microdonta ;* Torr. & Hook.; R0; 4; [C]; AF284950; AF285052 // *C. microptera c.f.;* Mack.; Hi; 4; [V]; -; AY779085 // *C. mira ;* Kük.; R0; 2; [C]; AF284944; AF285046 // *C. misera;* Buckley; W&S (just NCBI); 4; [C]; AY757534; AY757607 // *C. missouriensis;* P.E. Rothrock & Reznicek; Hi; 4; [V]; -; AY779121 // *C. molesta;* Mack. ex Bright; Hi; 4; [V]; -; DQ461143 // *C. molestiformis;* Reznicek & P.E. Rothrock; Hi; 4; [V]; -; DQ461144 // *C. monostachya;* A. Rich.; St; 0; [P]; -; AY241977 // *C. monostachya x runssoroensis 136;;* "Gehrke, Berit et al., BG-Af 136, Kenya, Mount Elgon National Park, Koroborte - Koitoboss track (Park Route), 3824m, N01°07'08.9“ E34°35'58.1“ (ZH); 0; [P]; EU288493*; EU288608* // *C. monostachya_069;* A. Rich.; "Gehrke, Berit et al., BG-Af 069, Kenya, Mount Kenya National Park, Naro Moru Route to Mackinders Camp, 3653m, S00°10'01.6“ E37°14'16.5“ (ZH); 0; [P]; EU288490*; EU288605* // *C. monostachya_095;* A. Rich.; "Gehrke, Berit et al., BG-Af 095, Kenya, Mount Kenya National Park, Sirimon Route path between Old Moses Camp and Shiptons Camp, 3699m, S00°04'02.1“ E37°17'51.3“ (ZH); 0; [P]; EU288491*; EU288606* // *C. monostachya_218;* A. Rich.; "Gehrke, Berit et al., BG-Af 218, Ethiopia, Bale Mountains National Park, Sinetti Plateau, 3800m, N06°53'15.1“ E39°54'23.7“ (ZH); 0; [P]; EU288492*; EU288607* // *C. monotropa_477;* Nelmes; "Gehrke, Berit et al., BG-Af 477, South Africa, Kwazulu Natal, Mont-aux-Source top plateau, 2843m, S28°45'08.8“ E28°52'58.4“ (ZH); 0; [C]; EU288494*; - // *C. montana;* L.; R0; 4; [C]; AF284877; AF284979 // *C. morrowii;* Boott in M.C.Perry; Guibert, Cyril CyG_BotGarden002, Botanical Garden of the University of

Zurich, (ZH); (1,2); [C]; EU288442*; EU288558* // *C. mossii 427;* Thunb.; "Gehrke, Berit et al., BG-Af 427, South Africa, Western Cape Province, dirt road between Wilderness and Sedgefield, (ZH) „ "; 0; [C]; EU288462*; - // *C. mucronata;* All.; Hb; 1; [C]; -; AY278257 // *C. muehlenbergii;* Schkuhr ex Willd.; W&S/ Fo; (4,5); [V]; AY757467; DQ115218 // *C. multicostata ;* Mack.; Hi; 1; [V]; -; AY779125 // *C. muricata;* L.; Ro; 1; [V]; AF284934; AF285036 // *C. muricata;* L.; R&F; 1; [P]; AF284934; AF285036 // *C. muskingumensis;* Schw.; Ha; 4; [V]; -; AY280541 // *C. nardina;* Fries; St; 4; [P]; -; AY241973 // *C. neurocarpa;* Maximovicz.; Fo; 2; [V]; -; DQ115222 // *C. neurophora;* Mack. in Abrams & *R.* S. Ferris; Fo; 4; [V]; -; DQ115224 // *C. nevadensis ;* L.; E; 3; [C]; -; DQ384172 // *C. nigra ;* (L.) Reichard; "Guibert, Cyril CyG2065 Switzerland, Graubünden, Alp Flix N46°32'03.20" E009°38'33.11" (ZH); (1,2,4); [C]; EU288443*; EU288559* // *C. nigromarginata ;* Schwein.; R&F; 4; [C]; -; AY325478 // *C. ninagonensis 349 ;* Nelmes; Gehrke, Berit et al., BG-Af 349, Uganda, Rwenzori Mts., between Nyabitaba Hut and John Matte Hut, (ZH); 0; [C]; EU288473*; EU288587* // *C. ninagonensis 371 ;* Nelmes; "Gehrke, Berit et al., BG-Af 371, Uganda, Rwenzori Mts., between Kitandara Hut and Guy Yeoman Hut after the Freshfield Pass , 3520m, N00°20'48.7" E29°55'10.3" (ZH); 0; [C]; EU288474*; EU288588* // *C. elgonensis 381 ;* Nelmes; "Gehrke, Berit et al., BG-Af 381, Uganda, Mgahinga Gorilla NP, Mt. Muhavura, 3248m, S01°22'26.6" E29°40'12.9" (ZH); 0; [C]; EU288475*; EU288589* // *C. normalis;* Mack.; Hi; 4; [V]; -; DQ461145 // *C. norvegica;* Retz.; Hb; (1,2,4); [C]; -; AY278264 // *C. novae-angliae;* Schw.; R&F; 4; [C]; -; AY325475 // *C. obispoensis;* Stacey; W&S (just NCBI); 4; [C]; AY757547; AY757620 // *C. obtusata;* Lilj.; St; (1,2,4); [P]; AF284865; AF284967 // *C. occidentalis ;* L.H. Bailey; Fo; 4; [V]; -; DQ115228 // *C. oklahomensis ;* Mack.; Fo; 4; [V]; -; DQ115230 // *C. olbiensis;* Jordan; Hb; 3; [C]; -; AY278282 // *C. oligocarpa ;* Willd.; W&S (just NCBI); 4; [C]; AY757542; AY757615 // *C. oligosperma;* Michx.; W&S (just NCBI); (2,4); [C]; AY757505; AY757578 // *C. opaca;* (F.J. Herm.) P.E. Rothrock & Reznicek; Hi; 4; [V]; -; AY779129 // *C. orizabae;* Liebm.; Hi; (4,5); [V]; -; AY779068 // *C. ornithopodioides;* Hausm.; Hb; (1,3); [C]; -; AY278268 // *C. oronensis;* Clokey; Hi; 4; [V]; -; AY779130 // *C. otrubae;* Podp.; Ro; (1,2,3); [V]; AF284894; AF284996 // *C. ovalis;* L.; "Guibert, Cyril CyG2059, Switzerland, Graubünden, Alp Flix N46°32'03.20" E009°38'33.11" (ZH); (1,2,3,4); [V]; EU288444*; EU288560* // *C. ovalis ;* Good.; Ro; (1,2,3,4); [V]; AF284900; AF28502 // *C. ovalis;* Gooden; St; (1,4); [P]; AF284900; AY280561 // *C. oxyandra;* Kudo; Ro; 2; [C]; AF284959; AF285061 // *C. ozarkana;* P.E. Rothrock & Reznicek; Hi; 4; [V]; -; AY779135 // *C. pachystachya ;* Cham. ex Steud.; Fo; (1,2,5); [V]; -; DQ115232 // *C. pairae ; ;* "Guibert, Cyril CyG2127, Switzerland, Bülach 669m N47°28'43.5" E008°25'36.1" (ZH); (1,3); [V]; EU288445*; EU288561* // *C. pallescens ;* L.; Ro; (1,2,4); [C]; AF284895; AF284997 // *C. panicea;* L.; Hb; (1,2); [C]; -; AY278284 // *C. paniculata;* L.; "Guibert, Cyril CyG2151, Switzerland, Graubünden, Alp Flix N46°32'03.20" E009°38'33.11" (ZH); (1,2); [V]; EU288446*; EU288562* // *C. pansa;* L.H. Bailey; Fo; 4; [V]; -; DQ115238 // *C. parallela;* (Laest.) Sommerf.; Ha; (1,2,3); [V]; -; AY280545 // *C. parviflora ;* Host; "Guibert, Cyril CyG2071, Switzerland, Graubünden, Alp Flix 2488m N46°31'8.7" E009°40'44.1" (ZH); 1; [C]; EU288447*; EU288563* // *C. pauciflora;* Lightf.; St; (1,2,4); [P]; AF284911; AF284983 // *C. paulo-vargasii ;* Luceno & Marin; E; 3; [C]; -; DQ384173 // *C. paupercula ;* Michx.; Hb; (1,2,4); [C]; AF284917; AY278292 // *C. peckii;* Howe; R&F; 4; [C]; -; AY325483 // *C. pedunculata;* Muehlenb.; Ro; 4; [C]; AF284867; AF284969 // *C. pendula;* Huds.; W&S (just NCBI); (1,2); [C]; AY757527; AY757600 // *C. pensylvanica;* Lam.; Ro; 4; [C]; AF284875; AF284977 // *C. pensylvanica_TLF;* Lam.; W&S (just NCBI); 4; [C]; AY757622; - // *C. peregrina_033 ;* Link; "Gehrke, Berit et al., BG-Af 033, Kenya, Aberdares National Park, Reedbuck Public Camp Site area, 2950m, S00°28'52.0" E36°43'48.5" (ZH); 0; [P]; EU288496*; EU288610* // *C. peregrina_105 ;* Link; "Gehrke, Berit et al., BG-Af 105, Kenya, Mount Kenya National Park, Sirimon Route, small stream below the bandas, 2606m, N00°03'25.7" E37°17'21.4" (ZH); 0; [P]; EU288497*; EU288611* // *C. perraudieriana ;* J. Gay ex Seub.; E; 3; [C]; -; DQ384177 // *C. petasata;* Dewey; Hi; 4; [V]; -; AY779138 // *C. petitiana_124;* A. Rich.; "Gehrke, Berit et al., BG-Af 124, Kenya, Mount Elgon National Park, Endebess Bluff track, 2700m,

N01°03'27“ E34°43'19“ (ZH) "; 0; [C]; EU288498*; EU288612* // *C. petitiana_308;* A. Rich.; "Gehrke, Berit et al., BG-Af 308, Malawi, Nyika National Park, road to Nganda Hill shortly before the summit, 2365m, S10°30'04.0“ E33°50'57.8“ (ZH); 0; [C]; EU288499*; EU288613* // *C. petitiana_337;* A. Rich.; "Gehrke, Berit et al., BG-Af 337, Southern Tansania, Iringa District, Kitulo Plateau, by the goat and cattle farm on the road from Mgeta, 2626m, S09°02'29.6“ E33°55'22.3“ (ZH); 0; [C]; EU288500*; EU288614* // *C. phaeocephala ;* Piper; Hi; 4; [V]; -; AY779139 // *C. phragmitoides_236;* Kük.; "Gehrke, Berit et al., BG-Af 236, Ethiopia, Bale Mountains National Park, Gaysay Valley, river on the road between Dodola and Dinsho, 3060m, N07°05'38.3“ E39°47'35.5“ (ZH); 0; [C]; EU288501*; EU288615* // *C. physodes;* M. Bieb.; Fo; (1,2); [V]; -; DQ115240 // *C. picta;* Steud.; Ro; 4; [C]; AF284948; AF285020 // *C. pilosa;* Scop.; Hb; (1,2); [C]; -; AY278286 // *C. pilulifera ;* L.; Ro; (1,3); [C]; AF284873; AF284975 // *C. pinetorum;* Liebm.; Ha; (4,5); [V]; -; AY280540 // *C. planata;* Franch. & Sav; Fo; 2; [V]; -; DQ115242 // *C. planostachys;* Kunze; Ro; (4,5); [C]; AF284932; AF285034 // *C. plantaginea;* Michx.; W&S (just NCBI); 4; [C]; AY757540; AY757613 // *C. podocarpa; R.* Br.; Ro; (2,4); [C]; AF284896; AF284998 // *C. polystachya;* Swartz ex Wahlenb.; Ro; (4,5); [I]; AF284912; AF285014 // *C. potosina;* Hemsl.; Fo; 4; [V]; -; DQ115244 // *C. praegracilis ;* Boott; Fo; (4,5); [V]; -; DQ115250 // *C. prairea;* Dewey; Fo; 4; [V]; -; DQ115252 // *C. prasina;* Wahlenb.; Ro; 4; [C]; AF284941; AF285043 // *C. praticola;* Rydb.; Hi; 4; [V]; -; AY779145 // *C. preslii;* Steud.; Hi; 4; [V]; -; AY779146 // *C. projecta;* Mack.; W&S/ Hi; 4; [V]; AY757487; AY779147 // *C. proxima_249;* Cherm.; "Gehrke, Berit et al., BG-Af 249, Madagascar, massif del'Ankaratra, around between Ambohimrandrana, 1632m, S19°21'37.2“ E47°18'52.5“ (ZH); 0; [I]; EU2885012*; - // *C. pseudobrizoides;* Clavaud; Ha; 1; [V]; -; AY280526 // *C. pseudocuraica;* Fr. Schmidt; Hi; 2; [V]; -; AY779148 // *C. pseudocyperus;* L.; Hb; (1,2,4); [C]; -; AY278295 // *C. pulicaris ;* L.; St; 1; [P]; -; AY242018 // *C. punctata;* Gaudin; E; (1,3); [C]; -; DQ384178 // *C. pyramidalis_299;* Kük.; "Gehrke, Berit et al., BG-Af 299, Madagascar, Ivohibe, western slope of the mountain, 1203m, S22°29'44.3“ E46°57'01.1“ (ZH); 0; [I]; EU288503*; EU288616* // *C. radiata;* (Wahlenb.) Small; Fo; 4; [V]; -; DQ115254 // *C. rariflora;* (Wahlenb.) Sm.; Hb; (1,2,4); [C]; -; AY278305 // *C. raynoldsii ;* Dewey; Hb; 4; [C]; -; AY278266 // *C. remota ;* L.; Ro; (1,2,3,6); [V]; AY757492; AY242001 // *C. renauldii_301;* H.Lév.; Gehrke, Berit et al., BG-Af 301, Madagascar, opposite the Parc National de Ranomafana, ca. 800m (ZH); 0; [I]; EU288504*; EU288617* // *C. reniformis;* (L.H. Bailey) Small; Hi; 4; [V]; -; AY779151 // *C. repens ;* Bell.; Ha; 1; [V]; -; AY280528 // *C. retrorsa;* Schwein.; W&S (just NCBI); 4; [C]; AY757504; AY757577 // *C. riparia;* Curtis; W&S (just NCBI); (1,2,5); [C]; AY757498; AY757571 // *C. rochebrunii;* Franch. & Sav; Fo; (2,6); [V]; -; DQ115260 // *C. roraimensis;* Steyerm.; Hi; 5; [V]; -; AY779152 // *C. rosea;* Schkuhr ex Willd.; W&S/ Fo; 4; [V]; AY757491; DQ115262 // *C. rossii;* Boott; Ro; 4; [C]; AF284870; AF284972 // *C. rostrata;* Stokes; "Linder, Peter PL7835 ZH, Switzerland, Horgen 526m N47°17'01.1“ E008°33'16.2“ "; (1,2,4); [C]; EU288448*; EU288564* // *C. rufina;* Drejer; W&S (just NCBI); (1,2,4); [C]; -; AY770485 // *C. rugosperma ;* Mack.; Ro; 4; [C]; AF284876; AF284978 // *C. runssoroensis_048;* K. Schum.; "Gehrke, Berit et al., BG-Af 048, Kenya, Aberdares National Park, top area on the Elephant, 3466m, S00°40'06.3“ E36°42'41.7“ (ZH); 0; [P]; EU288505*; EU288618* // *C. runssoroensis_062;* K. Schum.; "Gehrke, Berit et al., BG-Af 063, Kenya, Mount Kenya National Park, Naro Moru Route to Mackinders Camp, 3845m, S00°10'06.7“ E37°15'02.5“ (ZH); 0; [P]; EU288506*; EU288619* // *C. runssoroensis_369;* K. Schum.; "Gehrke, Berit et al., BG-Af 369, Uganda, Ruwenzori Mts., between Kitandara Hut and Guy Yeoman Hut at the sign of the Freshfield Pass , 4256m, N00°20'50.3“ E29°53'28.0“ (ZH); 0; [P]; EU288507*; EU288620* // *C. rutenbergiana_268;* Boeck.; "Gehrke, Berit et al., BG-Af 268, Madagascar, massif del'Ankaratra, Réserve Forestière et Piscicole de Manajakatompo, 1636m, S19°21'42.4“ E47°18'53.9“ (ZH); 0; [I]; -; EU288621* // *C. ruthii ;* Mack. in Britton; Fo; 4; [V]; -; DQ115264 // *C. sartwellii;* Dewey; Fo; 4; [V]; -; DQ115266 // *C. saxatilis;* L.; Taberlet et al. 2007, Hb; (1,2,4); [C]; DQ860539; AY278288 // *C. scabrata;* Schwein.; W&S (just NCBI); 4; [C]; AY757512; AY757585 // *C. scabrata;* Schwein.; W&S; 4; [V]; AY757512; AY757585 // *C.*

schottii; Dewey; Ro; 4; [C]; AF284935; AF285037 // *C. schweinitzii;* Dewey ex Schwein.; W&S (just NCBI); 4; [C]; AY757499; AY757572 // *C. scirpoidea ;* Michx.; Ro; (1,2,4); [C]; AF191820; AF285050 // *C. scita;* Maxim.; Senni et al. 2005; 2; [C]; AB219617; - // *C. scoparia;* Schkuhr ex Willd.; Hi; 4; [V]; -; AY779155 // *C. scopulorum ;* Holm; Ro; 4; [C]; AF284954; AF285059 // *C. secalina;* Willd.; Rogowski et al. 2007; (1,2); [C]; -; EF468658 // *C. sempervirens;* Vill.; "Guibert, Cyril CyG2174, Switzerland, Graubünden, Alp Flix 1993m N46°31'14.9" E009°39'24.5" (ZH); 1; [C]; EU288449*; EU288565* // *C. senanensis;* Ohwi; Fo; 2; [V]; -; DQ115268 // *C. seorsa ;* Howe in Gordinier & Howe; Fo; 4; [V]; -; DQ115270 // *C. serpenticola;* P. Zika; R&F; 4; [C]; -; AY325476 // *C. serratodens;* Boott; E; 4; [C]; -; DQ384183 // *C. shinnersii;* P.E. Rothrock & Reznicek;; 4; [V]; -; AY779157 // *C. shortiana;* Dewey; W&S (just NCBI); 4; [C]; AY757513; AY757586 // *C. siccata;* Dewey; Fo; 4; [V]; -; DQ115274 // *C. silicea;* Olney; Hi (only NCBI); 4; [V]; -; AY779159 // *C. simensis_019;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 019, Kenya, Aberdares National Park, area close to the Chania Camp site, 3557m, S00°19'58" E36°38'57.3" (ZH); 0; [C]; EU288508*; EU288623* // *C. simensis_063;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 063, Kenya, Mount Kenya National Park, Naro Moru Route to Mackinders Camp, 3845, S00°10'06.7" E37°15'02.5" (ZH); 0; [C]; EU288509*; EU288624* // *C. simensis_135;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 135, Kenya, Mount Elgon National Park, Koroborte - Koitoboss track (Park Route), 3824m, N01°07'08.9" E34°35'58.1" (ZH); 0; [C]; EU288510*; EU288625* // *C. simensis_202;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 202, Ethiopia, Bale Mountains National Park, Herenna Escarpment, 3343m, N06°46'50.5" E39°55'13.3" (ZH); 0; [C]; EU288511*; EU288626* // *C. simensis_359;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 359, Uganda, Rwenzori Mts., between John Matte Hut and Bukuju Hut between lower and upper Bigo Bog, 3450m, N00°23'15.9" E29°55'02.7" (ZH); 0; [C]; EU288512*; EU288627* // *C. simensis_382;* Hochst. ex A.Rich.; "Gehrke, Berit et al., BG-Af 382, Uganda, Mgahinga Gorilla NP, Mt. Muhavura, 3570m, S01°22'06.2" E29°40'19.7" (ZH); 0; [C]; EU288513*; EU288628* // *C. socialis;* Mohlenbr. & Schwegman; Fo; 4; [V]; -; DQ115278 // *C. sororia;* Kunth; Fo; 4; [V]; -; DQ115280 // *C. sp_203;* ; "Gehrke, Berit et al., BG-Af 203, Ethiopia, Bale Mountains National Park, Herenna Escarpment, 3343m, N06°46'50.5" E39°55'13.3" (ZH); 0; [C]; EU288514*; EU288629* // *C. sparganioides;* Muhl. ex Willd.; Fo; 4; [V]; -; DQ115282 // *C. specifica;* L.H. Bailey; Hi; 4; [V]; -; AY779160 // *C. sphaerogyna_256;* Baker; "Gehrke, Berit et al., BG-Af 256, Madagascar, massif de l'Ankaratra, around between Ambohimrandrana, 2265m, S19°20'05.7" E47°16'22.0" (ZH); 0; [C]; EU288516*; EU288632* // *C. sphaerogyna_290;* Baker; Gehrke, Berit et al., BG-Af 290, Madagascar, Parc National d'Andringitra, river (Riambavy) crossing beneath camp 2, 1950m (ZH); 0; [C]; EU288517*; EU288633* // *C. sphaerogyna_291;* Baker; Gehrke, Berit et al., BG-Af 291, Madagascar, Parc National d'Andringitra, river (Riambavy) crossing beneath camp 2, 1950m (ZH); 0; [C]; -; EU288634* // *C. spicata;* Huds.; Janyszek & Nuc 2007 / Fo; 1; [V]; EF514352; DQ115284 // *C. spicato-paniculata_470;* C.B. Clarke; "Gehrke, Berit et al., BG-Af 470, South Africa, Kwazulu Natal, Cathedral Peak Area, patch of naural montane forest around the chalet, 1610m, S28°56'16.2" E29°11'03.9" (ZH); 0; [I]; EU288518*; - // *C. spissa;* Bailey; Ro; 4; [C]; AF284938; AF285040 // *C. squarrosa;* L.; W&S(just NCBI); 4; [C]; AY757514; AY757587 // *C. stenantha;* Franch. & Sav.; Senni et al. 2005; 2; [C]; AB219618; - // *C. stenophylla;* Wahlenb.; Ha; (1,2,4); [V]; -; AY280535 // *C. stenoptila;* F.J. Herm.; Hi; 4; [V]; -; AY779161 // *C. sterilis;* Willd.; Fo; 4; [V]; -; DQ115286 // *C. steudneri_166;* Boeck.; "Gehrke, Berit et al., BG-Af 166, Kenya, Cherangani Hills, Cherangani Highway from Kapenguria to Iten, 5 km before Lobot, 2909m, N01°07'17.4" E35°31'85.3" (ZH); 0; [I]; EU288519*; EU288633* // *C. steudneri_196;* Boeck.; "Gehrke, Berit et al., BG-Af 196, Ethiopia, Menangesha Suba State Forest, *Juniperus* dominated forest, 2615m, N08°58'06.8" E38°34'00.3" (ZH); 0; [I]; EU288520*; EU288634* // *C. steudneri_327;* Boeck.; "Gehrke, Berit et al., BG-Af 327, Southern Tanzania, Mbeya District, Mbeya Peak area, saddle before the peak, 2740m, S08°50'25.0" E33°22'26.9" (ZH); 0; [I]; EU288521*; EU288635* // *C. stipata;* Muehlenb.; W&S/ Fo; (1,2,4); [V];

AY757471; DQ115288 // *C. straminea;* Willd. ex Schkuhr; Hi; 4; [V]; -; AY779163 // *C. straminiformis;* L.H. Bailey; Hi; 4; [V]; -; AY779164 // *C. stricta;* Lam.; D&B; 4; [C]; -; AY770486 // *C. stylosa; C.* A. Mey.; W&S (just NCBI); (1,2,4); [C]; AY757518; AY757591 // *C. subbracteata ;* Mack.; Hi; 4; [V]; -; AY779165 // *C. suberecta;* (Olney) Britton; Hi; 4; [V]; -; AY779166 // *C. subfusca;* Boott; Hi; 4; [V]; -; AY779167 // *C. subinflata_466 ;* Nelmes; "Gehrke, Berit et al., BG-Af 466, South Africa, Kwazulu Natal, Cathedral Peak Area, at the fishpond, 1435m, S28°56'53.7“ E29°11'56.4“ (ZH); 0; [C]; EU288522*; EU288638* // *C. supina;* Wahlenb.; St; (1,2,4); [P]; AF284897; AF284897 // *C. swanii;* (Fernald) Mack.; W&S (just NCBI); 4; [C]; AY757530; AY757603 // *C. sychnocephala;* J. Carey; Fo; 4; [V]; -; DQ115292 // *C. sylvatica;* Huds.; W&S (just NCBI); (1,2,3); [C]; AY757526; AY757599 // *C. tahoensis ;* Smiley; Hi; 4; [V]; -; AY779170 // *C. tasmanica;* Kük.; E; 6; [C]; -; DQ384184 // *C. tenax;* Chapm. ex Dewey; W&S (just NCBI); 4; [C]; AY757537; AY757610 // *C. tenera ;* Mack.; Hi; 4; [V]; -; DQ461149 // *C. teneriformis ;* Mack.; Hi; 4; [V]; -; AY779172 // *C. tenuiflora;* Wahlenb.; W&S (only NCBI); (1,2,4); [V]; AY757482; AY757427 // *C. tetrastachya ;* Scheele; Hi (only NCBI); 4; [V]; -; AY779173 // *C. texensis;* (Torrey ex L. H. Bailey) L.H. Bailey; Fo; 4; [V]; -; DQ115258 // *C. thunbergii ;* Steud.; D&B; (1,2,4); [C]; -; AY770488 // *C. tincta ;* (Fernald) Fernald; Hi; 4; [V]; -; AY779174 // *C. tomentosa;* L.; Ro; (1,2); [C]; AF284945; AF285047 // *C. tonsa var. tonsa;* (Fern.) E.P.Bicknell; R&F; 4; [C]; -; AY686723 // *C. torreyi;* Tuck.; Ro; 4; [C]; AF284949; AF285051 // *C. torta;* Boott; Ro; 4; [C]; AF284919; AF285021 // *C. triangularis ;* Boeck.; Fo; 4; [V]; -; DQ115296 // *C. tribuloides;* Wahlenb.; Hi; 4; [V]; -; AY779176 // *C. trichocarpa;* Muhl. ex Willd.; W&S (just NCBI); 4; [C]; AY757497; AY757570 // *C. trinervis;* Degl. in J.L.A.Loiseleur-Deslongchamps; D&B; (1,3); [C]; -; AY770491 // *C. trisperma;* Dewey; W&S/ Fo; 4; [V]; AY757483; DQ115298 // *C. troodi;* Turril; E; 3; [C]; -; DQ384186 // *C. tuckermanii;* Boott; W&S(just NCBI); 4; [C]; AY757500; AY757573 // *C. tumulicola;* Mack.; Fo; 4; [V]; -; DQ115300 // *C. turbinata;* Liebm.; R&F; 4; [C]; -; AY325465 // *C. typhina;* Michx.; W&S (just NCBI); 4; [C]; AY757515; AY757588 // *C. umbellata;* Willd.; R&F; 4; [C]; -; AY325486 // *C. umbrosa;* Host; Ro; (1,2); [C]; AF284940; AF28504 // *C. unilateralis ;* Mack.; Hi; 4; [V]; -; AY779177 // *C. vaginata;* Tausch; W&S (just NCBI); (1,2,4); [C]; AY757557; AY757629 // *C. vallicola;* Dewey; Fo; 4; [V]; -; DQ115302 // *C. vallis-rosetto_356;* K. Schum.; "Gehrke, Berit et al., BG-Af 356, Uganda, Rwenzori Mts., between Nyabitaba Hut and John Matte Hut, N00°21'00.2“ E29°56'15.1“ (ZH) "; 0; [C]; EU288523*; EU288639* // *C. vallis-rosetto_376;* K. Schum.; "Gehrke, Berit et al., BG-Af 376, Uganda, Rwenzori Mts., between Guy Yeoman Hut and Nyabitaba Hut, 3452m, N00°21'00.2“ E29°56'15.1“ (ZH) "; 0; [C]; EU288524*; EU288640* // *C. vernacula;* L. H. Bailey; Ro; 4; [V]; AF284920; AF285022 // *C. vesicaria;* L.; Hb; (1,2,3,4); [C]; -; AY278289 // *C. vestita;* Willd.; W&S (just NCBI); 4; [C]; AY757508; AY757581 // *C. vexans ;* F.J. Herm.; Hi; 4; [V]; -; AY779179 // *C. virescens;* Muhl. ex Willd.; W&S (just NCBI); 4; [C]; AY757533; AY757597 // *C. viridula;* Michx.; W&S (just NCBI) / Hb; (1,2,4); [C]; AY757524; AY278308 // *C. vixdentata ;* (Kük.) G.A. Wheeler; E; 5; [C]; -; DQ384189 // *C. vulpina;* L.; Ha; (1,2); [V]; -; AY280547 // *C. vulpinoidea;* Michx.; Ro; 4; [V]; AF284866; AF284968 // *C. wahuensis; C.* A. Mey.; Ro; 4; [C]; AF284921; AF285023 // *C. whitneyi;* Maack; Ro; 4; [C]; AF284951; AF285053 // *C. wiegandii;* Mack. in Britton; Fo; 4; [V]; -; DQ115310 // *C. wiluica;* Meinsh. ex Maack; Ro; (1,2); [C]; AF28490; AF285010 // *C. wootonii;* Mack.; Hi; 4; [V]; -; AY779181 // *C. xalapensis;* Kunth; Fo; (4,5); [V]; -; DQ115312 // *C. xerantica;* L.H. Bailey; Fo / Hi; 4; [V]; AF191821; AY779182 // *C. zuluensis_454 ;* C.B. Clarke; "Gehrke, Berit et al., BG-Af 454, South Africa, Kwazulu Natal, Bushmans Nek Area, ca. 3 km after main gate entrance along the river towards the east, 1770m, S29°50'46“ E29°12'48 (ZH); 0; [P]; EU288525*; EU288641* // Cym. *fraserianus ;* Mack.; St; 4; [P]; AF284955; AF285057 // Eriophorum; *vaginatum;* L.; W&S (just NCBI) /St; (0,1,2,4,5); -; AY757692; AY242008 // K. *capillifolia;* (Decne.) *C.* B. Clarke; St; 2; [P]; AF284882; AF284984 // K. *fragilis;* C.B. Clarke; Fo; 2; [P]; AF164945; - // K. *gammiei;* C.B. Clarke; Fo; 2; [P]; AF164944; - // K. *laxa;* Nees in R.Wight; Fo; 2; [P]; AF164943; - // K. *myosuroides;* (Vill.) Fiori; St; (1,2,4); [P]; AF284883; AY242036 // K. *royleana;* (Nees) Boeck.; Fo; 2; [P]; AF164947; - // K. *sibirica;* (Turcz. ex Ledeb.) Boeck;

St; (1,2,4); [P]; AF284884; AF284986 // K. *simpliciuscula;* (Wahlenb.) Mack.; Fo / St; (1,2,4); [P]; AF164948; AY241971 // K. *simpliciuscula;* (Vill.) Fiori; "Guibert, Cyril CyG2135, Switzerland, Graubünden, Alp Flix 1993m N46°31'14.9“ E009°39'24.5“ (ZH); (1,2,4); [P]; EU288540*; EU288566* // K. *simpliciuscula;* (Vill.) Fiori; Guibert, Cyril CyG2070 Switzerland (ZH); (1,2,4); [P]; EU288541*; - // K. *uncinioides;* (Boott) C.B. Clarke; Fo; 2; [P]; AF164946; - // S. *451;;* "Gehrke, Berit et al., BG-Af 451, South Africa, Kwazulu Natal, between Kokstad and Underberg along R617, bridge over Mzuntlava River, 1490m, S30°23'04.8“ E29°26'57.9“ (ZH); 0; [P]; EU288526*; EU288642* // S. *452;;* "Gehrke, Berit et al., BG-Af 452, South Africa, Kwazulu Natal, Bushmans Nek Area, Caravan Park near Wildlife Services Centre, close to the little waterfall, 1705m, S29°50'46.7“ E29°12'57.2“ (ZH); 0; [P]; EU288527*; EU288643* // S. *467;;* "Gehrke, Berit et al., BG-Af 467, South Africa, Kwazulu Natal, Cathedral Peak Area, footpath towards fern forest, 1333m, S28°56'55.0“ E29°11'48.6“ (ZH); 0; [P]; EU288528*; EU288644* // S. *469;;* "Gehrke, Berit et al., BG-Af 469, South Africa, Kwazulu Natal, Cathedral Peak Area, patch of naural montane forest around the chalet, 1372m, S28°56'16.2“ E29°11'03.9“ (ZH); 0; [P]; EU288529*; - // S. *473;;* "Gehrke, Berit et al., BG-Af 473, South Africa, Kwazulu Natal, Cathedral Peak Area, at the fishpond, 1330m, S28°56'55“ E29°11'48 (ZH); 0; [P]; EU288530*; - // S. *474;;* "Gehrke, Berit et al., BG-Af 474, South Africa, Kwazulu Natal, Mont-aux-Source area, close to the Witsieshoek Mountain Resort, 2180m, S28°41'20.1“ E28°53'51.5“ (ZH); 0; [P]; EU288531*; EU288645* // S. *479;;* "Gehrke, Berit et al., BG-Af 479, South Africa, Kwazulu Natal, Golden Gate National Park, Echo Ravine trail, 1895m, S28°30'18.5“ E28°37'16.4“ (ZH); 0; [P]; EU288532*; EU288646* // S. *480;;* "Gehrke, Berit et al., BG-Af 480, South Africa, Kwazulu Natal, Golden Gate National Park, 1844m, S28°30'30.0“ E28°37'05.8“ (ZH); 0; [P]; EU288533*; EU288647* // S. *burkei;* C.B. Clarke; St; 0; [P]; AF284922; AF284922 // S. *ecklonii_433;* Nees ; "Gehrke, Berit et al., BG-Af 433, South Africa, Eastern Cape Province, between Grahamstown and Port Alfred towards East London, Shaw Park near Fish River Lighthouse, S33°30'01.0“ E27°03'66.5“ (ZH); 0; [P]; EU288535*; EU288649* // S. *filiforme ;* Kük.; Fo / St; 0; [P]; AF164951; AY242020 // S. *lehmannii ;* (Nees) Steud.; W&S/ St; 0; [P]; AY757560; AY242026 // S. *ludwigii;* Hochst.; Fo; 0; [P]; AF164949; - // S. *madagascariensis 275;* Cherm.; Gehrke, Berit BG-Af 275 ZH; 0; [P]; EU288536*; - // S. *rufum 160 (cf sparteum);* C.B. Clarke; "Gehrke, Berit et al., BG-Af 160, Kenya, Saiwa Samp National Park, 1893m, N01°11'53.3“ E35°12'85.4“ (ZH); 0; [P]; EU288537*; EU288648* // S. *rufum_338 ;* Nees; "Gehrke, Berit et al., BG-Af 338, Southern Tansania, Iringa District, Kitulo Plateau, wet area with many Lobelia stands just below first grassland peak by the goat and cattle farm on the road from Mgeta, 2626m, S09°02'29.6“ E33°55'22.3“ (ZH); 0; [P]; EU288537*; EU288650* // S. *sp_185;;* "Gehrke, Berit et al., BG-Af 185, Ethiopia, Addis Ababba, Entoto Hills , assigned area for the Botanical Garden, 2879m, N09°04'57.9“ E38°43'17.1“ (ZH); 0; [P]; EU288538*; - // S. *sparteum;* (Wahlenb.) *C.* B. Clarke; W&S/ St; 0; [P]; AY757561; AY242022 // S. *sparteum_193;* (Wahlenb.) *C.* B. Clarke; "Gehrke, Berit et al., BG-Af 193, Ethiopia, Menangesha Suba State Forest, Juniperus dominated forest, 2731m, N08°58'01.8“ E28°33'55.3“ (ZH); 0; [P]; EU288539*; EU288651* // Scirpus *microcarpus;* Presl; Ro; (1,2,4); -; AF284859; AF284961 // U. *phleoides;* (Cav.) Pers.; Fo / Ro; (4,5); [P]; AF164931; AY012670 // U. *uncinata;* (L.f.) Kük. in Engler; St; 6; [P]; AF284886; AF284988 //

RANUNCULUS *Trautvetteria carolinensis;* Vail; Xi; 4; R.; AF007946; AH007301 // *Trautvetteria grandis;* Honda; Hö; 4; R.; AF007945; AY680202 // T*rautvetteria japonica;* Sieb. & Zuc*C.* Xi; 2; R.; AF007944; AH007297 // *Callianthemoides semiverticillatus ;* (Philippi) Tamura; Pa/ Hö; 5; R.; AY954236; AY680199 // *Ceratocephala falcata;* (L.) Pers.; Pa/ Hö; (1,2,3); R.; AY954229; AY680191 // *Ceratocephala orthoceras;* D*C.* Pa/ Hö; (1,2); R.; AY954230; AY680190 // *Halerpestes cymbalaria;* (Pursh) Greene; Pa/ Hö; (2,4,5); R.; AY954237; AY680196 // *Myosurus minimus;* L.; Hang et al. 2001; (1,2,3,4,6); R.; -; AJ414344 // *Peltocalathos baurii;* (MacOwan) M.Tamura; Pa/ Hö; 0; R.; AY954235; AY680200 // *Peltocalathos baurii_462;* (MacOwan) M.Tamura; Berit Gehrke et al. BG-Af 462, South Africa, Kwazulu Natal,

Drakensberg, at the top of Sani Pass, 2834m, 29°35'31.0“S 29°16'55.1"E; 0; R.; -; EU288398* // *R. aberdaricus;* Ulbr.; Berit Gehrke et al. BG-Af 101, Kenya, Sirimon Route, small stream below the bandas 2571m, S00°00'18.4" E37°14'22.0" (ZH); 0; R.; EU288371*; - // *R. abortivus;* L.; Pa/ Hö; 4; R.; AY954126; AY680048 // *R. acaulis;* DC. Lo; 6; R.; -; AF323319 // *R. acetosellifolius;* Boiss.; Pa/ Hö; 3; R.; AY954226; AY680075 // *R. aconitifolius;* L.; Pa/ Hö; (1,3); R.; AY954217; AY680081 // *R. acris;* L.; Pa/ Hö; (1,2,3,); R.; AY954199; AY680167 // *R. adoneus;* A. Gray; Hö; 4; R.; -; AY680030 // *R. aduncus;* Gren & Godr.; Pa/ Hö; (1,3); R.; AY954143; AY680088 // *R. allemannii;* Br.-Bl.; Hö; 1; R.; -; AY680039 // *R. alpestris;* L.; Pa/ Hö; 1; R.; AY954221; AY680078 // *R. altaicus;* Laxm.; Pa/ Hö; 2; R.; AY954116; AY680112 // *R. amerophyllus;* F. Muell.; Hö; 6; R.; -; AY680146 // *R. amplexicaulis;* L.; Pa/ Hö; 3; R.; AY954223; AY680071 // *R. anemoneus;* F. Muell.; Lo; 6; R.; -; AF323273 // *R. apenninus;* (Chiov.) Pign.; Pa/ Hö; (1,3); R.; AY954150; AY680091 // *R. apiifolius;* Pers. (=Aphanostemma apiifolia (Pers.) St.-Hil.; Pa/ Hö; 5; R.; AY954140; AY680092 // *R. arcticus;* Richards.; Pa/ Hö; (1,2,4); R.; AY954125; AY680049 // *R. baldshuanicus;* Regel ex Kom.; Pa/ Hö; (1,3); R.; AY954195; AY680174 // *R. basilobatus ;* H. Eichler ex P. van Royen; Hö; 6; R.; -; AY680131 // *R. bequaertii;* De Wild.; Berit Gehrke et al. BG-Af 358, Uganda, Ruwenzori Mts., between John Matte Hut and Bukuju Hut, 3441m, N00°22'00.4“ E29°55'23.5“ (ZH); 0; R.; EU288372*; EU288399* // *R. bilobus;* Bertol.; Pa/ Hö; 1; R.; AY954220; AY680077 // *R. biternatus;* Sm.; Hö; 5; R.; -; AY680061 // *R. bonariensis ;* Poir.; Hö; 5; R.; -; AY680183 // *R. borealis;* Trautv.; Hö; (1,2); R.; -; AY680168 // *R. brassii;* H. Eichler; Hö; 6; R.; -; AY680127 // *R. brevifolius subsp. brevifolius;* Ten.; Pa/ Hö; 1; R.; AY954212; AY680187 // *R. breyninus;* Cr.; Pa/ Hö; (1,2); R.; AY954172; AY680116 // *R. brotherusii ;* Freyn; Hö; 2; R.; AY954119; AY680037 // *R. buchanani;* Hook. f.; Lo; 6; R.; -; AF323280 // *R. bulbosus subsp. bulbosus;* L.; Pa/ Hö; (1,2,3); R.; AY954188; AY680124 // *R. bullatus;* L.; Pa/ Hö; 3; R.; AY954161; AY680114 // *R. calandrinioides;* Oliver; Hö; (1,2,3); R.; -; AY680073 // *R. cantoniensis;* DC. Hö; 2; R.; -; AY680126 // *R. cappadocicus;* Willd.; Pa/ Hö; (1,2); R.; AY954173; AY680117 // *R. caprarum;* Skottsb.; Hö; 5; R.; -; AY680151 // *R. cardiophyllus;* Hook. f.; Pa/ Hö; 4; R.; AY954124; AY680045 // *R. carinthiacus;* Hoppe; Pa/ Hö; (1,3); R.; AY954124; AY680093 // *R. carpaticola ;* Soó; Pa/ Hö; 1; R.; AY954145; AY680041 // *R. carpaticus;* Herbich; Pa/ Hö; 1; R.; AY954111; AY680096 // *R. carpinetorum;* Hörandl & Guterm.; Pa/ Hö; 6; R.; AY954154; AY680031 // *R. cassubicifolius;* W. Koch; Pa/ Hö; 1; R.; AY954112; AY680040 // *R. chilensis;* DC:; Pa/ Hö; 5; R.; AY954179; AY680157 // *R. chius;* DC. Hö; (1,2,3); R.; AY954201; AY680176 // *R. cicutarius;* Schlecht.; Hö; (1,2,3); R.; AY954167; AY680103 // *R. circinatus;* Sibth.; Lo; 1; R.; -; AF323321 // *R. collinus;* DC. Hö; 6; R.; AY954137; AY680059 // *R. colonorum;* Endl.; Hö; 6; R.; -; AY680139 // *R. cornutus;* DC:; Hö; (1,2,3); R.; -; AY680153 // *R. cortusifolius;* Willd.; Hö; 3; R.; AY954160; AY680101 // *R. crassipes;* Hook. f.; Hö; 6; R.; -; AY680060 // *R. creticus;* Sieb. ex Steud.; Pa; 3; R.; AY954163; AY954239 // *R. crithmifolius;* Hook. f.; Lo; 6; R.; -; AF323311 // *R. crypthantus;* Milne-Redh. & Turrill; Berit Gehrke et al. BG-Af 142, Kenya, Mount Elgon National Park, eastern side of the Caldera near Koitoboss, 3841m, N01°07'08.9“ E34°35'58.1“ (ZH); 0; R.; EU288373*; - // *R. cupreus;* Boiss. & Heldr.; Pa; 3; R.; AY954164; AY954240 // *R. diffusus;* DC. Li; 2; R.; -; DQ410722 // *R. dissectifolius;* Benth.; Hö; 6; R.; -; AY680144 // *R. eichleranus ;* Briggs; Hö; 6; R.; -; AY680138 // *R. enysii;* T. Kirk; Lo; 6; R.; -; AF323316 // *R. eschscholtzii;* Schlecht.; Hö; (1,2,4); R.; AY954127; AY680050 // *R. ficaria;* Lambinon; Hö; (1,2,3); R.; AY954232; AY680192 // *R. ficariifolius;* Sm.; Li; 2; R.; -; DQ410729 // *R. flagelliformis;* Sm.; Hö; 5; R.; AY954208; AY680182 // *R. flammula;* L.; Hö; (1,2,3,4); R.; AY954204; AY680185 // *R. fluitans;* Lam.; Hö; (1,3); R.; AY954129; AY680069 // *R. fuegianus;* Speg.; Pa/ Hö; 5; R.; AY954136; AY680064 // *R. garganicus;* Ten.; Pa/ Hö; 3; R.; AY954165; AY680107 // *R. gayeri;* Soó; Hö; 2; R.; -; AY680028 // *R. gelidus;* Kar. & Kir.; Pa/ Hö; 2; R.; AY954114; AY680054 // *R. godleyanus;* Hook. f.; Lo; 6; R.; -; AF323309 // *R. gouanii;* Willd.; Pa/ Hö; 1; R.; AY954151; AY680098 // *R. gracilipes;* Hook. f.; Hö; 6; R.; -; AY680120 // *R. grahamii;* Petrie; Lo; 6; R.; -; AF323286 // *R. gramineus;* L.; Pa/ Hö; 1; R.; AY954227; AY680076 // *R. granatensis ;* Boiss.; Pa/ Hö; 3; R.; AY954197; AY680165 // *R. grandiflorus;* L.; Pa/ Hö; (1,2); R.; AY954203;

AY680053 // *R. grandifolius;* C.A. Mey.; Hö; 2; R.; -; AY680169 // *R. graniticola ;* Melville; Hö; 6; R.; -; AY680141 // *R. gregarius;* Brot.; Pa/ Hö; 3; R.; AY954159; AY680100 // *R. gunnianus;* Hook. f.; Lo; 6; R.; -; AF323298 // *R. haastii;* Hook. f.; Lo; 6; R.; -; AF323284 // *R. hirtellus;* Royle; Pa/ Hö; 2; R.; AY954120; AY680038 // *R. hybridus;* Biria; Pa/ Hö; 1; R.; AY954211; AY680189 // *R. hydrophilus ;* Bunge; Hö; 5; R.; -; AY680181 // *R. hyperboreus ;* Rottb.; Pa/ Hö; (1,2,4); R.; AY954135; AY680065 // *R. illyricus;* L.; Pa/ Hö; (1,2,3); R.; AY954162; AY680119 // *R. induratus;* ined.; Hö; 6; R.; -; AY680125 // *R. insignis;* Hook. f.; Pa/ Hö; 6; R.; AY954141; AF323306 // *R. japonicus;* Thunb.; Pa/ Hö; 2; R.; AY954200; AY680164 // *R. kochii;* Ledeb.; Pa/ Hö; 1; R.; AY954231; AY680193 // *R. kuepferi;* Greuter & Burdet; Pa; 1; R.; AY954214; AY954241 // *R. lappaceus;* Sm.; Hö; 6; R.; -; AY680140 // *R. lapponicus;* L.; Pa/ Hö; (1,2,4); R.; AY954234; AY680194 // *R. lateriflorus;* DC. Pa/ Hö; (1,2,3); R.; AY954209; AY680179 // *R. lingua;* L.; Pa/ Hö; (1,2,3); R.; AY954206; AY680184 // *R. lomatocarpus;* Fisch & Mey.; Pa; (1,2,3); R.; AY954178; AY954178 // *R. longicaulis ;* C.A. Mey.; Pa/ Hö; 2; R.; AY954117; AY680051 // *R. lowii;* Stapf; Hö; 6; R.; -; AY680128 // *R. lyallii;* Hook. f.; Pa/ Lo; 6; R.; AY954142; AF323276 // *R. macranthus;* d'Urv.; Leebens-Mack et al. 2005; 4; R.; DQ069586; - // *R. marginatus;* d'Urv.; Pa/ Hö; (1,2,3); R.; AY954177; AY680150 // *R. marschlinsii;* Steud.; Pa/ Hö; 1; R.; AY954147; AY680089 // *R. melzeri;* Hörandl & Guterm.; Hö; 2; R.; -; AY680036 // *R. membranaceus;* Royle; Hö; 2; R.; -; AY680056 // *R. meyeri ;* Harv.; Berit Gehrke et al. BG-Af 463, South Africa, Kwazulu Natal, at the top of Sani Pass, 2834m, S29°35'31.0“ E29°16'55.1“ (ZH); 0; R.; EU288374*; EU288400* // *R. micranthus;* Nutt.; Pa/ Hö; 4; R.; AY954113; AY680042 // *R. millanii;* F. Muell.; Hö; 6; R.; -; AY680134 // *R. millefoliatus;* Vahl; Pa/ Hö; 3; R.; AY954166; AY680108 // *R. minutiflorus;* Bert. ex Phil.; Hö; 5; R.; -; AY680156 // *R. monophyllus ;* L.; Hö; (1,2); R.; -; AY680043 // *R. montanus;* Willd.; Pa/ Hö; 1; R.; AY954149; AY680094 // *R. muelleri;* Benth.; Hö; 6; R.; -; AY680143 // *R. multifidus;* Forssk.; Pa/ Hö; 0; R.; AY954183; AY680162 // *R. multifidus 110;* Forssk.; Berit Gehrke et al. BG-Af 110, Kenya, Mount Kenya National Park, Sirimon Route, 2571m, S00°00'18.4“ E37°14'22.0“ (ZH); 0; R.; EU288376*; EU288402* // *R. multifidus 154;* Forssk.; Berit Gehrke et al. BG-Af 154, Kenya, Saiwa Samp National Park, 1893m, N01°11'53.3“ E35°12'85.4“ (ZH); 0; R.; EU288378*; EU288404* // *R. multifidus 179;* Forssk.; Berit Gehrke et al. BG-Af 179, Kenya, road between Eldoret and Kabernet, 1973m S00°38'11.7“ E35°31'12.7“ (ZH); 0; R.; EU288379*; EU288405* // *R. multifidus 215;* Forssk.; Berit Gehrke et al. BG-Af 215, Ethiopia, Bale Mountains National Park, village entrance of Goba on road from Robe 2559m, N07°01'25.5“ E39°58'53.6“ (ZH); 0; R.; EU288380*; EU288406* // *R. multifidus 342 ;* Forssk.; Berit Gehrke et al. BG-Af 342, Southern Tansania, Morogoro District, Uluguru Mountauins, Lukwangule Plateau, road between Tchenzema and Nyandira, ca. 1700; 0; R.; EU288381*; EU288407* // *R. multifidus 348;* Forssk.; Berit Gehrke et al. BG-Af 348, Uganda, Ruwenzori Mts., between Gate Entrance and Nyabitaba, 2100m, N00°21'25.6“ E30°01'05.0“ (ZH) "; 0; R.; EU288382*; EU288408* // *R. multifidus 428 ;* Forssk.; Berit Gehrke et al. BG-Af 428, South Africa, Western Cape Province, dirt road between Wilderness and Sedgefield; 0; R.; EU288383*; - // *R. multifidus 478;* Forssk.; Berit Gehrke et al. BG-Af 478, South Africa, Kwazulu Natal, Mont-aux-Source top plateau, 2843, S28°45'08.8“ E28°52'58.4“ (ZH); 0; R.; EU288384*; EU288409* // *R. multiscapus ;* Hook. f.; Hö; 6; R.; -; AY680133 // *R. muricatus;* L.; Pa/ Hö; (1,2,3); R.; AY954191; AY680148 // *R. nanus;* Hook. f.; Hö; 6; R.; -; AY680142 // *R. neapolitanus;* Ten.; Pa/ Hö; 3; R.; AY954187; AY680123 // *R. nemorosus;* DC. Pa; 1; R.; AY954184; AY954184 // *R. niphophilus ;* Briggs; Hö; 6; R.; -; AY680145 // *R. nivalis;* L.; Pa/ Hö; (1,2,4); R.; AY954123; AY680046 // *R. nivicola;* Hook. f.; Lo; 6; R.; -; AF323308 // *R. notabilis;* Hörandl & Guterm.; Pa/ Hö; 1; R.; AY954115; AY680033 // *R. occidentalis;* Nutt.; Hö; 4; R.; -; AY680171 // *R. ollissiponensis;* Pers.; Pa/ Hö; 3; R.; AY954157; AY680109 // *R. ophioglossifolius ;* Vill.; Pa/ Hö; (1,2,3); R.; AY954207; AY680180 // *R. oreophytus 035;* Delile; Berit Gehrke et al. BG-Af 035, Kenya, Aberdares National Park, Karuru Waterfall, 2703m, S00°29'26.3“ E36°38'04.0“ (ZH); 0; R.; -; EU288410* // *R. oreophytus 072 ;* Delile; Berit Gehrke et al. BG-Af 072, Kenya, Mount Kenya National Park, area around Naro Moru Bandas, 3142m, S00°10'06.8“

E37°13'06.0“ (ZH); 0; R.; EU288385*; EU288411* // *R. oreophytus 209;* Delile; Berit Gehrke et al. BG-Af 209, Ethiopia, Bale Mountains National Park, Herenna Escarpment, 3343m, N06°46'50.5“ E39°55'13.3“ (ZH); 0; R.; -; EU288412* // *R. oreophytus 344;* Delile; Berit Gehrke et al. BG-Af 344, Southern Tansania, Morogoro District, Uluguru Mountauins, Lukwangule Plateau, 2412m, S07°07'15.5“ E37°36'21.1“ (ZH) "; 0; R.; EU288386*; EU288413* // *R. oreophytus 351 ;* Delile; Berit Gehrke et al. BG-Af 351, Uganda, Ruwenzori Mts., near John Matte Hut, in moist patches near boggs; 0; R.; EU288387*; EU288414* // *R. pachyrrhizus;* Hook. f.; Lo; 6; R.; -; AF323295 // *R. pallasii;* Schlecht.; Pa/ Hö; (1,2,4); R.; AY954233; AY680195 // *R. paludosus;* Poir.; Pa/ Hö; 3; R.; AY954155; AY680102 // *R. pannonicus;* Soó; Hö; 1; R.; -; AY680032 // *R. papulentus;* Melville; Pa/ Hö; 6; R.; AY954138; AY680058 // *R. parnassifolius;* L.; Pa/ Hö; 1; R.; AY954224; AY680072 // *R. peduncularis;* Sm.; Pa/ Hö; 5; R.; AY954180; AY680154 // *R. peltatus;* Moench; Pa/ Hö; (1,3); R.; AY954131; AY680068 // *R. penicillatus;* (Dum.) Bab.; Pa/ Hö; (1,3); R.; AY954130; AY680070 // *R. pensylvanicus;* L. f.; Pa/ Hö; 4; R.; AY954190; AY680147 // *R. pilisiensis ;* Soó; Hö; 2; R.; -; AY680034 // *R. pimpinellifolius;* Hook. f.; Hö; 6; R.; -; AY680136 // *R. pinguis;* Hook. f.; Lo; 6; R.; -; AF323299 // *R. pinnatus 247;* Poir.; Berit Gehrke et al. BG-Af 247, Madagascar, massif del'Ankaratra, around between Ambohimrandrana, 1635m, S19°21'20.6“ E47°18'49.8“ (ZH); 0; R.; EU288388*; EU288415* // *R. platanifolius;* L.; Pa/ Hö; (1,3); R.; AY954216; AY680080 // *R. plebeius;* DC. Hö; 6; R.; -; AY680137 // *R. polii;* Franch. ex Forb. & Hemsl.; Li; (1,3); R.; -; DQ410717 // *R. pollinensis ;* Chiov.; Pa/ Hö; (1,3); R.; AY954152; AY680097 // *R. polyanthemos;* L.; Pa/ Hö; (1,2,3); R.; AY954185; AY680121 // *R. praemorsus;* H.B. & K. ex. DC:; Hö; 5; R.; -; AY680161 // *R. prasinus;* Menadue; Hö; 6; R.; -; AY680057 // *R. propinquus;* C.A. Mey.; Pa/ Hö; 2; R.; -; AY680170 // *R. pseudohirculus;* Schrenk ex Fisch. & C.A. Mey.; Hö; 2; R.; AY954118; AY680111 // *R. pseudolowii ;* H. Eichler; Hö; 6; R.; -; AY680130 // *R. pseudomillefoliatus;* Grau; Pa/ Hö; 3; R.; AY954156; AY680110 // *R. pseudomontanus;* Schur; Pa/ Hö; (1,3); R.; AY954146; AY680090 // *R. pseudotrullifolius;* Skottsb.; Pa/ Hö; 5; R.; AY954139; AY680203 // *R. psilostachys;* Grieseb.; Pa/ Hö; 3; R.; AY954170; AY680106 // *R. pygmaeus;* Wahlenb.; Pa/ Hö; (1,2,4); R.; AY954122; AY680044 // *R. rarae;* Exell; Berit Gehrke et al. BG-Af 304, Malawi, Malosa Plateau near Zomba, path across the plateau, 1548m, S15°18'03.8“ E35°17'38.3“ (ZH); 0; R.; EU288389*; EU288416* // *R. rarae 322;* Exell; Berit Gehrke et al. BG-Af 322, Malawi, Nyika National Park, Chelinda River Road, shortcut from the Camp to the airstrip, 2345m, S10°30'63.7“ E33°48'60.1“ (ZH); 0; R.; EU288390*; EU288417* // *R. recens;* T. Kirk; Lo; 6; R.; -; AF323320 // *R. reptans;* L.; Pa/ Hö; (1,2,4); R.; AY954205; AY680186 // *R. rufosepalus ;* Franch.; Pa/ Hö; 2; R.; AY954121; AY680047 // *R. rumelicus;* Grieseb.; Pa/ Hö; 3; R.; AY954168; AY680104 // *R. sardous;* Cr.; Pa/ Hö; (1,3); R.; AY954186; AY680122 // *R. sartorianus ;* Boiss. & Heldr.; Pa/ Hö; 3; R.; AY954148; AY680095 // *R. saruwagedicus;* H. Eichler; Hö; 6; R.; -; AY680129 // *R. scapigerus;* Hook. f.; Hö; 6; R.; -; AY680135 // *R. scrithalis;* P.J. Garnock-Jones; Lo; 6; R.; -; AF323305 // *R. seguieri;* Vill.; Pa/ Hö; (1,3); R.; AY954215; AY680079 // *R. serbicus;* Vis.; Pa/ Hö; 3; R.; AY954196; AY680166 // *R. sericocephalus;* Hook. f.; Hö; 6; R.; -; AY680155 // *R. serpens;* G.López; Pa; (1,3); R.; -; AY954243 // *R. shuichengensis;* L. Liao; Li; 2; R.; -; DQ410719 // *R. sieboldii;* J.Q.Fu; Li; 2; R.; -; DQ410726 // *R. silerifolius;* H. Lév.; Li; 2; R.; AB069847; DQ410725 // *R. simensis;* Fresen.; Berit Gehrke et al. BG-Af 231 Ethiopia, Bale Mountains National Park, road between Goba and Sinetti Plateau, 2961m, N06°56'25.4“ E39°57'33.2“ (ZH); 0; R.; EU288391*; EU288418* // *R. sp. 126;* ; Berit Gehrke et al. BG-Af 126, Kenya, Mount Elgon National Park, Endebess Bluff track, 2700m, N01°03'27“ E34°43'19“ (ZH); 0; R.; EU288397*; - // *R. sphaerospermus;* Boiss. & Blanche; Pa/ Hö; (1,3); R.; AY954132; AY680066 // *R. spicatus;* Desf.; Pa; 3; R.; AY954158; AY954244 // *R. sprunerianus;* Boiss.; Pa/ Hö; 3; R.; AY954169; AY680105 // *R. stagnalis 357;* Hochst. ex A. Rich.; Berit Gehrke et al. BG-Af 357, Uganda, Ruwenzori Mts., between John Matte Hut and Bukuju Hut, at the upper end of the “Lower Bigo Bog”, 3441m, N00°22'00.4“ E29°55'23.5“ (ZH); 0; R.; -; EU288420* // *R. stagnalis 228;* Hochst. ex A. Rich.; Berit Gehrke et al. BG-Af 228, Ethiopia, Bale Mountains National Park, Sinetti Plateau, 3887m, N06°51'11.3“

E39°56'30.3“ (ZH); 0; R.; EU288392*; EU288419* // *R. subscaposus ;* Hook. f.; Hö; 6; R.; -; AY680132 // *R. tanguticus;* (Finet & Gagnep.) Hao; Hö; 2; R.; -; AY680055 // *R. tembensis ;* Hochst. ex A. Rich.; Berit Gehrke et al. BG-Af 210, Ethiopia, Bale Mountains National Park, Herenna Escarpment, 3343m, N06°46'50.5“ E39°55'13.3“ (ZH); 0; R.; EU288393*; EU288421* // *R. ternatus;* DC. Li; 2; R.; -; DQ410716 // *R. thora;* L.; Pa/ Hö; 1; R.; AY954210; AY680188 // *R. traunfellneri;* Schott; Pa; 1; R.; AY954222; AY954245 // *R. trichophyllus;* Chaix.; Pa/ Hö; (0,1,2,3,4,6); R.; AY954133; AY680067 // *R. trigonus;* Hand.- Mazz.; Li; 2; R.; -; DQ410724 // *R. trilobus;* Desf.; Pa/ Hö; 3; R.; AY954176; AY680149 // *R. trullifolius;* Hook. f.; Hö; 5; R.; -; AY680159 // *R. vaginatus;* Hand.-Mazz.; Li; 2; R.; -; DQ410720 // *R. variabilis;* Hörandl & Guterm.; Hö; 1; R.; -; AY680029 // *R. velutinus;* Schur; Pa/ Hö; 3; R.; AY954198; AY680173 // *R. venetus;* Huter & Landolt; Pa/ Hö; 1; R.; AY954144; AY680087 // *R. verticillatus;* Eastw.; Lo; 6; R.; -; AF323303 // *R. villarsii;* DC. Pa/ Hö; 1; R.; AY954153; AY680099 // *R. vindobonensis;* Hörandl & Guterm.; Hö; 1; R.; -; AY680035 // *R. viridis;* H.D. Wilson & P.J. Garnock-Jones; Lo; 6; R.; -; AF323297 // *R. volkensii 102;* Engl.; Berit Gehrke et al. BG-Af 102, Kenya, Mount Kenya National Park, Sirimon Route, small stream below the bandas, 2571m, S00°00'18.4“ E37°14'22.0“ (ZH); 0; R.; EU288394*; EU288422* // *R. volkensii 143;* Engl.; Berit Gehrke et al. BG-Af 143, Kenya, Mount Elgon National Park, eastern side of the Caldera near Koitoboss, 3841m, N01°07'08.9“ E34°35'58.1“ (ZH); 0; R.; EU288395*; EU288423* // *R. volkensii 353;* Engl.; Berit Gehrke et al. BG-Af 353 Uganda, Ruwenzori Mts., between John Matte Hut and Bukuju Hut, shortly before the lower Bigo Bog, 3277m, N00°22'50.2" E29°56'32.5"(ZH); 0; R.; EU288396*; EU288424* // *R. weyleri;* Mares; Pa; 3; R.; AY954189; AY954246

Appendix 2:

Overview of *Carex*, *Ranunculus* and *Alchemilla*: total number of taxa and number of accessions (for *Carex*: Ford et al. 2006, Starr et al. 2004, Roalson et al. 2001, Yen and Olmstead 2000, Reznicek 1990, Ball 1990; for *Ranunculus*: Paun et al. 2006, Hörandl et al. 2005). Higher number of taxa in the separate analyses can occur because taxa with incongruent placement were removed from the dataset before the combined analysis.

taxa	total number of species	distribution	status of the genus/ subgenus	number of taxa in the analysis combined (cpDNA/ nrDNA)	African accessions/ **African taxa in analysis**/ *taxa in Africa*
Carex	1500	worldwide especially in temperate areas, centre of species diversity in North America (420 spp.) and Himalaya/East Asia (450 spp.)	paraphyletic, including *Indocarex* and *Vigneastra*	280 (76/260) (14 *Indocarex)*	33 / **22** / *26 (-40)* +18 / **14** / *27 (-40) (Indocarex)*
Primocarex / *Psyllophora*	60	cold temperate areas, centre of species diversity Circumarctic; *Schoenoxiphium* mainly in temperate Southern Africa	polyphyletic, including *Cymophyllus, Kobresia, Schoeno-xiphium* and *Uncinia*	62 (67/69)	27 / **4** / 5 +20/ **14** / *18 (Schoenoxiphium)*
Vignea	420	worldwide especially in temperate areas, centre of species diversity in North America (180 spp.) and northern Eurasia (100 spp.)	monophyletic	214 (213/75)	11 / **5** / *3 (-8)*
Ranunculus.	600	worldwide especially in temperate and boreal areas	monophyletic	223 (229/156)	27 / **16** / 20
Alchemilla	1000	worldwide with a centre of diversity in Eurasia (subgenus *Alchemilla*), Andean (subgenus *Lachemilla*), the Mediterranean (subgenus *Aphanes*) and the African Mountains (Afromilla clade in the subgenus *Alchemilla*)	the genus and all four major clades are monophyletic	100 (94/93)	26 / **27** / 32

Appendix 3:

Discussion on African high mountain clades in the molecular phylogenetic reconstructions.

Notes: Author names of taxa included in the molecular phylogenetic analyses can be found in Appendix 1. The trees of the molecular phylogenetic analyses of separate markers can be obtained from the author upon request. Bootstrap support values (bs) and Bayesian clade credibilities (cc) are given were applicable.

Carex

Historically, at least four colonisation events into the African high mountains were expected for *Carex (Hedberg 1965).* More could have been expected if sectional relationships were trusted as a reflection of relatedness. Molecular phylogenetic analyses and parsimony optimisations indicate that there have been at least thirteen independent immigration events of *Carex* into the African high mounatins.

Carex* subgenus *Carex:

Subgenus *Carex* is the largest clade in *Carex*. It either includes the subgenus *Indocarex* or it is sister to *Indocarex*. A number of taxa that have previously been placed in other subgenera are here placed in subgenus *Carex*, for example *C. scirpoidea* and *C. picta (Hendrichs et al. 2004b; Yen & Olmstead 2000).* Many sections described by Kükenthal (1909) and other authors appear to be supported by molecular phylogenetic analyses unlike those in the other subgenera (Ford et al. 2006; Roalson et al. 2001; Starr et al. 2004).

(i) **Acutiformis clade:** *C. acutiformis* occurs in Europe and Africa, whereas *C. mossii* and *C. austro-africana* are found only in South Africa. Together they form a weak to moderate supported clade (69 bs in the combined and 89 bs in the ITS analysis) sister to *C. amplifolia,* a North-American member of the Sect. *Anomalae* Carey in A. Gray. This section of about 30 species is strongly developed in eastern Asia, with several species in Australasia and two species in North America. Only few examples from eastern Asia are included and we consider the source area of the *C. acutiformis* clade therefore as ambiguous even though the ancestral area reconstruction is indicating a North American origin.

(ii) ***C. bequaertii:*** There is strong support (85 bs and 1.00 cc) for a sister species relationship of the East African *C. bequaertii* to the morphologically similar, but smaller, *C. pendula*. Together they form a clade sister to a clade of Eurasian *C. sylvatica* and *C. cretica*. *C. bequaertii* is therefore likely to have been derived from a Eurasian ancestor.

(iii) **Cognata clade***: C. cognata, C. subinflata, C. sphaerogyna and C. phragmitoides* form a moderate to weakly supported clade (70 bs but c.c. below 0.95) sister to other species of the section Pseudo-cypereae Tuckerm. Pseudo-cypereae is distributed in Europe, western North America and the South American Andes. The Cognata clade was optimised as been derived from a North American ancestor. Based on taxonomy this clade contains at least two more taxa in Africa (*C. drakensbergensis* C.B. Cl. and *C. cognata* Kunth var. *congolensis* Turill).

(iv) ***Johnstonii****: C. johnstonii* is a slender species that occurs widespread in the upper parts of the Afromontane forests. Morphologically it is most similar to *C. fastigiata* Franch from Central China. Unfortunately *C. fastigiata* was not included in the analyses and the sister relationship with *C. capillaris,* which was retrieved in a number of most parsimonious tree, was not supported overall. Nevertheless, parsimony optimisations show a Eurasian ancestral area.

(v) **Madagascariensis clade:** The Madagascan taxa *C. humberti* and *C. madagascariensis* form a well-supported clade (100 bs and 1.00 cc). They were placed by Kükenthal in the section Praelongae Kük. and are most likely closely related to *C. papilossisima* from Sao Hill in Southern Tanzania. Their sister relationship with the South African *C. austro-africana* is not supported (58 bs and cc below 0.95). The ancestral area optimisation indicates a North American origin. However, in some of the most parsimonious trees *C. nigra* was placed sister to the Madagascariensis clade and the ancestral area was optimised as Eurasia.

(vi) ***Monotropa****:* The South African *C. monotropa* is well supported (91 bs and 1.00 cc) as sister to northern European *C. hostiana* and this clade is well supported (99 bs and 1.00 cc) as sister to the rest of the *Carex flava* complex. Parsimony optimisations indicate a Eurasian ancestral area.

(vii) **Simensis clade**: The Simensis clade is one of the biggest clades of *Carex* in Africa. We have included eight of the postulated ten species, but species delimitation in this group is difficult. The inclusion of *C. clavata* from South Africa is only supported in the *trn*LF analysis, which contains only few species in this part of the phylogeny compared to the number of taxa for which ITS sequence data is available (see also Escudero et al. 2007). A sister species relationship to *C. punctata,* from Europe and North African, is not supported in the combined analysis but moderately supported in the *trn*LF analysis (87 bs). Parsimony optimisations indicate a Eurasian (Mediterranean) ancestral area.

Carex* subgenus *Primocarex/Psyllophora:

The subgenus is paraphyletic and includes other members of the tribe Cariceae, such as the monophyletic genus *Uncinia*, the polyphyletic *Korbresia* and *Elyna*, the monospecific genus *Cymophyllus* and *Schoenoxiphium (Starr et al. 2004)*.

(viii) **Monostachya clade:** *C. monostachya and C. runssoroensis* are dominant species in moist parts of the Afroalpine areas. The species can form hybrid swarms (Hedberg 1957) and constitute a clade sister to *C. capitata* (99 bs and 0.99 cc), a widespread species found from Northern Eurasia, sub-Arctic America to high altitude South America. Together they are sister to *C. obtusata* (75 bs and 1.00 cc) that has a circumboreal distribution. Parsimony optimisations indicate a North American ancestral area for the Monostachya clade.

(ix) ***Peregrina****: C. peregrina* occurs not only in East Africa and Ethiopia but also on the Macaronesian Islands, the Azores and North Africa. It is well supported as sister to the European *C. pulicaris* (60 bs and 1.00 cc in the combined and 100 bs in the ITS analysis). They are a sister to *C. acicularis* from New Zealand (93 bs and 1.00 cc) and in turn sister to *C. phyllostachys* from temperate western Asia (91 bs in the ITS and 1.00 cc in the combined analysis). The Parsimony optimisations retrieve a equivocal result for the Adams consensus. However, many of the most parsimonious tree indicate a Eurasian ancestral area for *C. peregrina*.

(x) ***Schoenoxiphium:*** Monophyly of the genus *Schoenoxiphium* is well supported in the Bayesian analyses (0.99 cc) but not recovered in the parsimony analysis. It is sister to a clade that includes *C. peregrina* and allies as well as the South African species *C. zuluensis*. *C. zuluensis* is morphological very similar to *Schoenoxiphium,* and its placement outside the Schoenoxiphium clade is not supported. *Schoenoxiphium* is most widespread in southern Africa but also occurs in eastern Africa and Madagascar. The monophyly of the Schoenoxiphium clade including *C. zuluensis* was neither confirmed nor rejected by parametric bootstrapping. More data are needed to confirm this relationship and the monophyly of *Schoenoxiphium.*

Carex* subgenus *Vignea:

The subgenus *Vignea* is the second largest clade in *Carex* (Hendrichs et al. 2004a; Hipp et al. 2006). However, the African high mountain clades are relatively species poor compared to those in subgenus *Carex*: the *C. conferta* clade consists of three species, whereas the *C. glomerabilis* and *C. erythrorrhiza* do not seem to have speciated in Africa.

(xi) **Conferta clade:** *C. conferta*, *C. leptosaccus* and *C. lycurus* form a moderate to well supported clade (81 bs and 0.99 cc). They are most likely closest related to the eastern North American *C. crus-corvi* and a clade comprising the European *C. appropinquata*, and the Australian/New Zealand *C. appressa.* But relationship in the clade is unresolved. Parsimony optimisations indicated a northern American ancestral area.

(xii) ***Erythrorrhiza:*** *C. erythrorrhiza* is well supported as sister to *C. divisa*, a species native to Europe and western Asia that has been introduced in

Australia and North America from Europe. Parsimony optimisations indicate a western Eurasian ancestral area.

(xiii) ***Glomerabilis**:* The South African species *C. glomerabilis* is weakly supported as sister to *C. canariensis* from the Macaronesian islands (65 bs and cc below 0.95). They seem to be closely related to the European species group of *C. muricata* including *C. divulsa* that is native in Macaronesia, Europe, Mediterranean to western Himalaya and introduced elsewhere. Parsimony optimisations indicate a western or eastern Eurasian ancestral area.

Ranunculus:

Our results are congruent with the molecular phylogenetic analyses published previously (Hörandl et al. 2005; Paun et al. 2005). For *Ranunculus*, taxonomic affinities of the African high mountain taxa and therefore the number of colonisation events have been more uncertain. Engler (1892) recognised seven of the twelve of the African high mountain species in *Ranunculus* to have Eurasian (mainly Mediterranean and Himalayan) affinities, two are South African related and two are generally temperate or uncertain. Hedberg (1957) lists all alpine taxa of *Ranunculus* as belonging to the pan-temperate element but mentions that their placement might change when the taxonomy of the group is better known. We inferred four to six immigrations from Eurasia, and none from either North America or South America. Akin to *Carex*, 30-40% of all of *Ranunculus* taxa in the African sky-islands are of Eurasian affinity. Molecular phylogenetic analyses show at least six clades of which only four are well supported. *Peltocalathos baurii* is an additional member of the Ranunculaceae present in the high mountains of African (it is endemic to the Drakensbergen). *P. baurii* is represented in the molecular phylogeny by two accessions, however it was only treated as an outgroup and not included in further discussion.

(i) ***Meyeri**:* The position of *R. meyeri,* a mainly southern African species, is weakly supported within a clade of *R. lingula*, *R.flammula* and *R. reptans* that occur in wetlands worldwide and *R. ficariifolia* (98 bs). It is closely related to *R. volkensii*. Parsimony optimisations indicate eastern Eurasia as the ancestral area. However, if *R. meyeri* and *R. volkensii* form a clade the ancestral area can also be reconstructed equivocal either as eastern or western Eurasia with two dispersals out of Africa instead of two independent migrations into Africa.

(ii) **Multifidus clade**: The Multifidus clade is well supported (97 bs and 0.98 cc). It comprises *R. multifidus,* which is found through out Africa*, R. pinnatus* from Madagascar and the East African *R. aberdaricus* and *R. bequaertii* (see also comment below).

(iii) ***R. oreophytus* and *R. rarae**:* In the matK analysis *R. oreophytus, R. rarae* and the Multifidus clade form a polytomy. In the combined analyses however, *R. oreophytus, R. rarae* form clade in a polytomy including Mediterranean and

Asian species, a South American clade and the Multifidus clade. It is not possible to determine with certainty the ancestral area, however two independent immigrations from European lowlands is possible. The parsimony optimisation indicates eastern Eurasia as ancestral area for both taxa.

→ The placement (within a larger clade) of the Multifidus- and Oreophytus-clades has no support. In some of the most parsimonious trees these two clades form a clade together with *R. praemorsus* and *R. vaginatus*. The ancestral area reconstruction optimises the ancestral node of this clade as African meaning at least one dispersal out of Africa for the clade of *R. praemorsus* and *R. vaginatus*. However the Adams consensus indicates two independent dispersal events for the Multifidus- and Oreophytus-clade. More data (taxa and potentially markers) is required to test this potential out of Africa migration.

(iv) ***Stagnalis:*** Comprises *R. cryptanthus, R. cuneilobus, R. simensis, R. stagnalis* and *R. tembensis* and might include two more taxa from Ethiopia that were not sampled. The clade is weakly to well supported (67 bs and 1.00 cc) and most likely sister *R. velutinus* and *R. serbicus* (no support) and is member of a clade with mainly European lowland species (100 bs and 1.00 cc). The parsimony optimisation indicates the Mediterranean as the ancestral area.

(v) ***R. tichophyllus****: R. tichophyllus* is an aquatic species distributed throughout the world. We were not able to sample it in Africa and the species is therefore represented by a European accession.

(vi) ***R. volkensii****: R. volkensii* is an alpine species sister to *R. lateriflorus, a* species distributed in the wetlands worldwide including North Africa. It is nested within a clade of wetland species with entire to more or less dentate leaves. The parsimony optimisation indicates eastern Eurasia as the ancestral area (but see also *R. meyeri*).

Alchemilla:

For results of the molecular phylogenetic analyses of the two marker regions *trn*L-*trn*F (cpDNA) and ITS (nrDNA) see Gehrke et al. (2008). The only African example of the subgenus *Aphanes* (*A. bachitii*) is only found in Ethiopia. It is rarely collected and was not included in this study. It does represent a second introduction of *Alchemilla*. However, we can not make any inferences as to its status or source of origin. All other African taxa form a monophyletic clade called the Afromilla clade (which includes only taxa which formerly belong to the subgenus *Alchemilla* in opposite to A. *bachitii* which is a member of the subgenus *Aphanes*). No morphological characters are known to distinguish the Afromilla clade from the Eurasian Alchemilla species even though the monophyly of the Afromilla clade is very well supported. Opposite to this lack of character to distinguish these two

clade, the Aphanes clade is characterised by the single extrose stamen inserted at the inner side of the discus, members of the Afromilla- and the Eurasian *Alchemila*- clades posses usually four introse stamens inserted at the outer side of the discus and the fourth group, the Lachemilla clade, which had previously been thought to be very closely related to the Aphanes clade, has two extrose stamens inserted at the inner side of the discus. Molecular phylogenetic reconstructions point towards a closer relationship of the Aphanes clade with the Eualchemilla clade than which are sister to either the Lachemilla clade or a combined clade of the Lachemilla and the Afromilla clade. We feel therefore confident that the Aphanes clade will hold to be monophyletic and that *A. bachitii* is a member of the Aphanes clade and that this is a monophyletic clade not part or sister to the Afromilla clade and is therefore representing a separate colonisation event.

Engler (1892) suggested at least three different affinities between members of the Afromilla clade and Eurasian *Alchemilla* taxa. Hedberg (1957) did not go into details of taxonomic relationships. The monophyly of the African *Alchemilla* taxa is well supported (see Gehrke et al. 2008), and it can thus be assumed that they have derived from a single colonisation event. Ancestral area reconstruction is not possible due to under-sampling in the outgroup and the uncertain relationships between the Afromilla clade, *Lachemilla* and the combined *Alchemilla-Aphanes*-clade. However, an eastern Asian origin is likely given the distribution of the outgroup. Reconstruction of the ancestral area mapped onto the Adams consensus is ambiguous. However, a Eurasian origin is reconstructed unambiguously if eastern and western Eurasia including the Mediterranean is coded as a single area (data not shown).

Appendix 4:

Parametric bootstrap analyses:

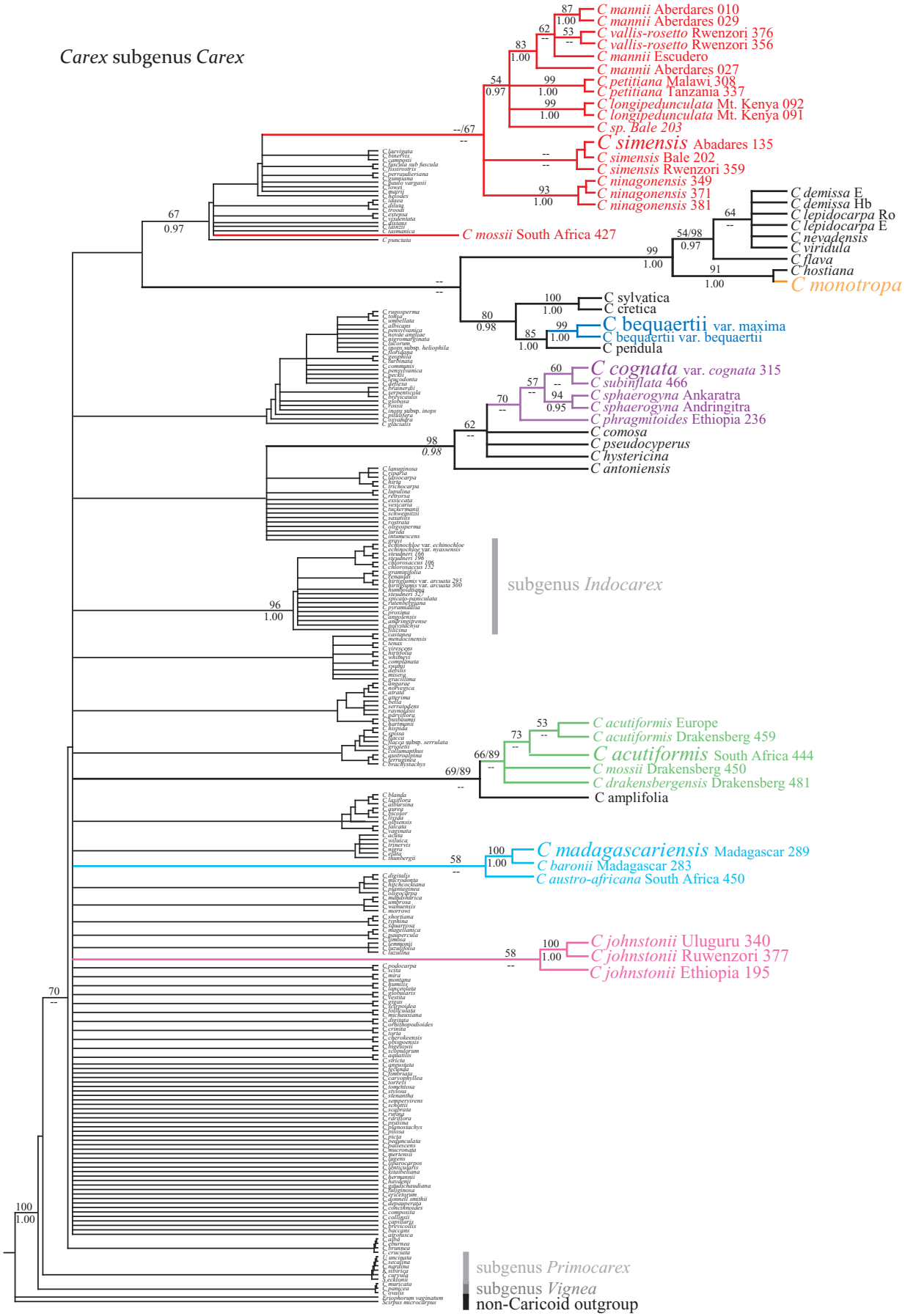
For the parametric bootstrap analyses (Huelsenbeck et al. 1996) we calculated the null distributions of tree-lengths by creating 100 simulated datasets based a tree in which all African accessions, or a subset of taxa in each subgenus, were constrained to be monophyletic (see below). For dataset simulation, we first estimated the best fitting substitution model parameters given the constrained topologies using Modeltest v3.7 (Posada & Crandall 1998) implemented in PAUP* (Swofford 2001). The parameters were then used to calculate branch lengths for the constrained trees, which we used to create 100 simulated data matrices of nucleotide sequence data using SeqGen (Rambaut & Grassly 1997). Length-differences between the constrained and unconstrained trees for each simulated matrix were calculated in PAUP* using heuristic searches of 1000 replicates, random sequence addition, tree-bisection-reconnection (TBR) branch swapping, MULTREE on (keeping multiple, equally parsimonious trees), saving a maximum of 50 trees per replicate. The calculated length-differences constitute the null distribution, against which the differences in the tree lengths of the original dataset were plotted (again unconstrained tree length minus constrained tree length). Where this difference falls outside the 95% confidence interval, it cannot be attributed to stochasticity and must be considered as significant, i.e. monophyly of the clade as defined by the constraint can be rejected.

The table below shows the results of parametric bootstrap analyses to test hypotheses of monophyly for different combinations of clades. The P-values represent the proportion of the 100 simulated data sets which yielded a length difference equal to or greater than the empirical difference between the hypothesis constrained and unconstrained tree. Tree length of the original dataset unconstraint (tlenU) – tree length of the original dataset enforcing a constraint (tlenC). This value is compared to the p-value of the normal distribution of the number of categories represented by the differences tree length of the constrained and unconstrained data in the simulated matrices (categories).

Constraint	Substitution model under GTR+I+G	P	tlenU–tlenC (categories)	Monophyly rejected/ accepted
all African taxa in Vignea	Lset Base=(0.3035 0.1959 0.2038) Rmat=(1.0000 2.1656 0.8559 0.8559 4.2447) Shape=0.6475 Pinvar=0.4162;	p<0.0001	31 (6)	rejected
Conferta/Glomerabilis	Base=(0.3035 0.1959 0.2038) Rmat=(1.0000 2.1656 0.8559 0.8559 4.2447) Shape=0.6475 Pinvar=0.4162	p<0.0001	15 (6)	rejected
Conferta/Erythrorrhiza	Lset Base=(0.3093 0.2028 0.1974) Rmat=(0.7261 1.9160 0.7463 0.7443 3.5904) Shape=0.6693 Pinvar=0.4233;	p<0.0001	19 (5)	rejected
Erythrorrhiza/Glomerabilis	Base=(0.3076 0.2019 0.1992) Rmat=(0.7517 1.9297 0.7527 0.7417 3.6744) Shape=0.6614 Pinvar=0.4244;	p<0.0001	31 (4)	rejected
all African taxa in Psyllophora	Base=(0.2993 0.2052 0.2030) Rmat=(0.6301 1.4413 0.5213 0.6293 3.4184) Shape=0.5998 Pinvar=0.4641;	p<0.0001	47 (6)	rejected
Schoenoxiphium/ *C. peregrina* /Acicularis clade	Lset Base=(0.2975 0.2182 0.2057) Rmat=(0.5758 1.3571 0.5264 0.5588 3.2186) Shape=0.6045 Pinvar=0.4521;	?	1 (1)	ambiguous
Schoenoxiphium	Lset Base=(0.2991 0.2165 0.2043) Rmat=(0.5654 1.3420 0.5137 0.5339 3.2414) Shape=0.5971 Pinvar=0.4531;	p>0.5	0 (5)	accepted
all African taxa in Carex	Lset Base=(0.3049 0.2049 0.2006)	p<0.0001	122 (6)	rejected

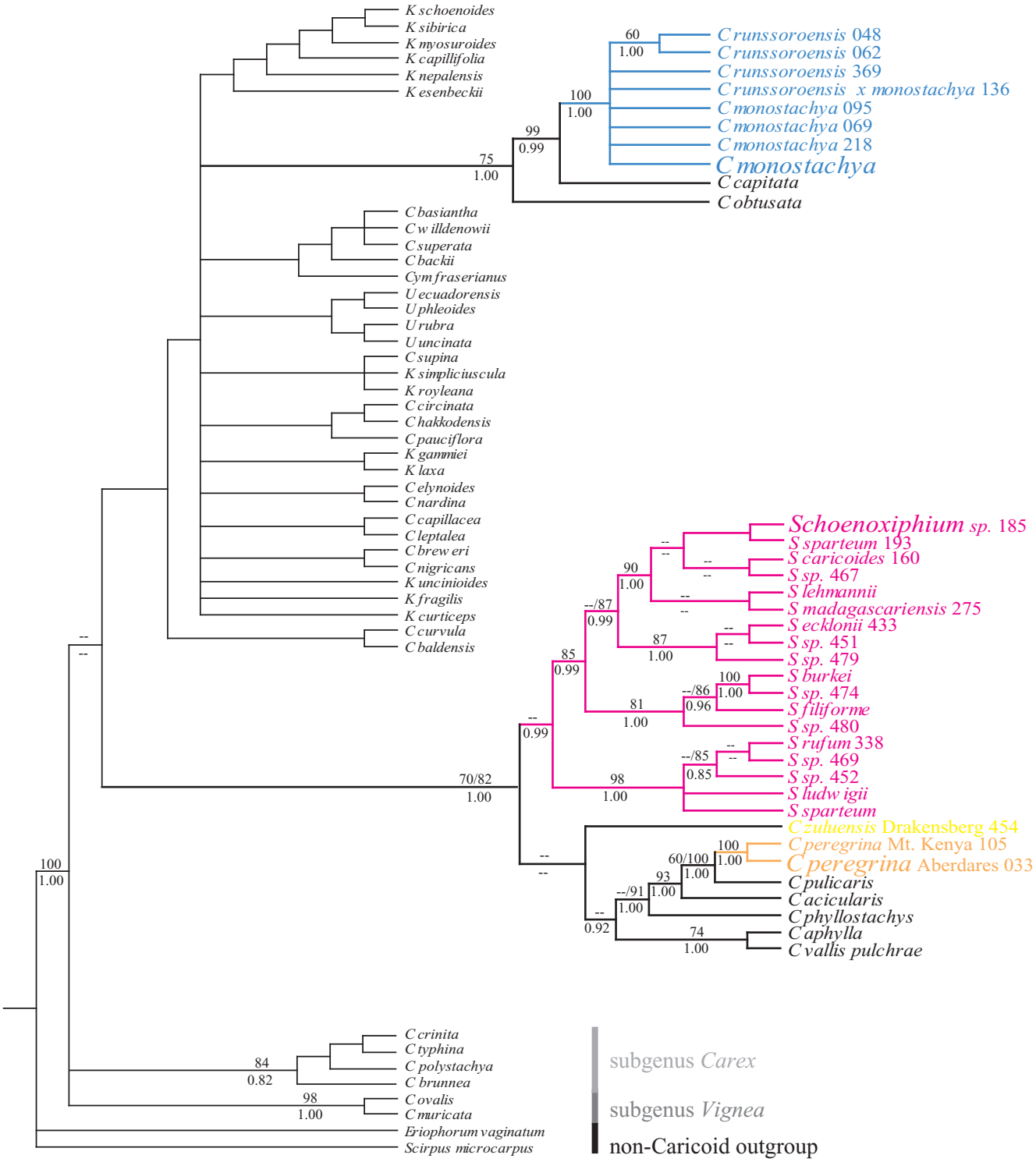
	Rmat=(0.7048 2.2859 0.5088 0.6443 3.2459) Shape=0.5376 Pinvar=0.3926;			
C. bequaertii/ *C. monotropa*	Lset Base=(0.3087 0.2060 0.1986) Rmat=(0.6546 2.2593 0.4958 0.6657 3.4195) Shape=0.4664 Pinvar=0.3959;	p<0.0001	(3)	rejected
Acutiformis clade/ Madagascariensis clade	Lset Base=(0.3008 0.2053 0.2068) Rmat=(0.7148 2.2307 0.5242 0.6709 3.5152) Shape=0.5223 Pinvar=0.3964;	p<0.0001	19 (6)	rejected
C. johnstonii/*Bequaertii* clade	Lset Base=(0.3023 0.2062 0.2018) Rmat=(0.7289 2.3583 0.5414 0.6587 3.3676) Shape=0.5408 Pinvar=0.3873;	p<0.01	14 (5)	rejected
Simensis clade	Lset Base=(0.2915 0.2060 0.2157) Rmat=(1.0000 2.5936 0.6853 0.6853 4.0508) Shape=0.5552 Pinvar=0.3842;	?	0 (1)	ambiguous
all Ranunculaceae	Lset Base=(0.3141 0.1676 0.1711) Rmat=(1.3612 2.7757 0.7879 0.8777 3.4593 Shape=0.7203 Pinvar=0.2929;	p<0.0001	123 (3)	rejected
Multifidus	Lset Base=(0.3145 0.1659 0.1717) Rmat=(1.3791 2.7256 0.8036 0.9001 3.4695) Shape=0.7247 Pinvar=0.2720;	p>0.5	-1 (2)	accepted
Multifidus/Oreophytus	Lset Base=(0.3157 0.1639 0.1711) Rmat=(1.3987 2.7167 0.8000 0.9128 3.5085) Shape=0.7282	p>0.5	-1 (0-2)	accepted

	Pinvar=0.2729;			
R. volkensii/*R. meyeri*	Lset Base=(0.3164 0.1648 0.1704) Rmat=(1.3826 2.6979 0.7990 0.9095 3.5002) Shape=0.7277 Pinvar=0.2732;	p>0.5	0 (3)	accepted

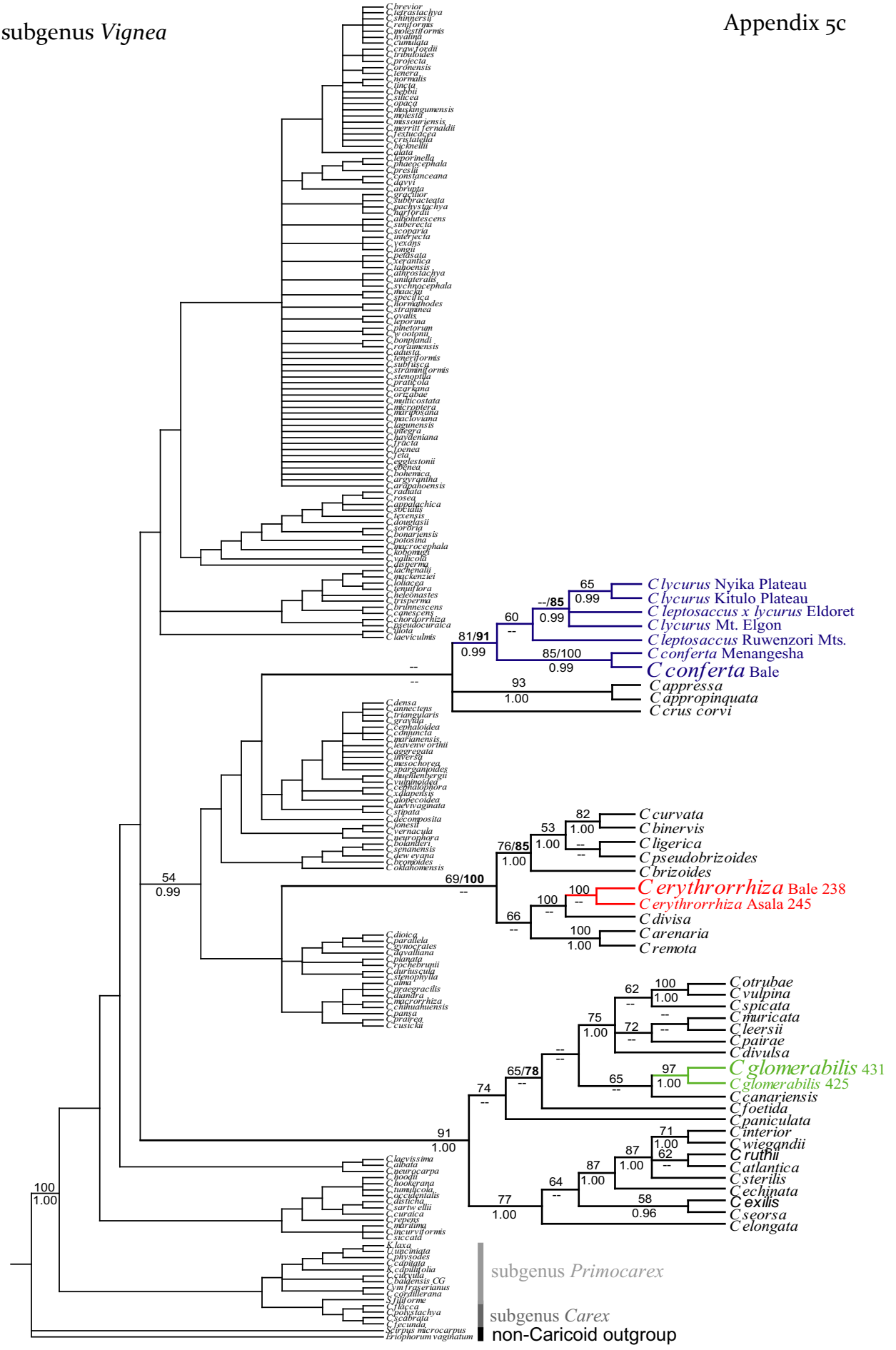


Strict consensus tree of *Carex* subgenus *Carex* based on the combined nuclear ITS and trnLF dataset reconstructed using parsimony; bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches (only for clades containing accessions from Africa, indicated in bold, African accessions in colour). Where higher support values were achieved in separate analyses of the individual markers, these are given after a slash in bold

Carex subgenus *Primocarex* and other caricoid Cariceae



Strict consensus tree of *Carex* subgenus *Primocarex* (= sect. *Psyllophora*) based on the combined nuclear ITS and trnL-F dataset reconstructed using parsimony; bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches (only for clades containing accessions from Africa, indicated in bold, African accessions in colour). Where higher support values were achieved in separate analyses of the individual markers, these are given after a slash in bold.

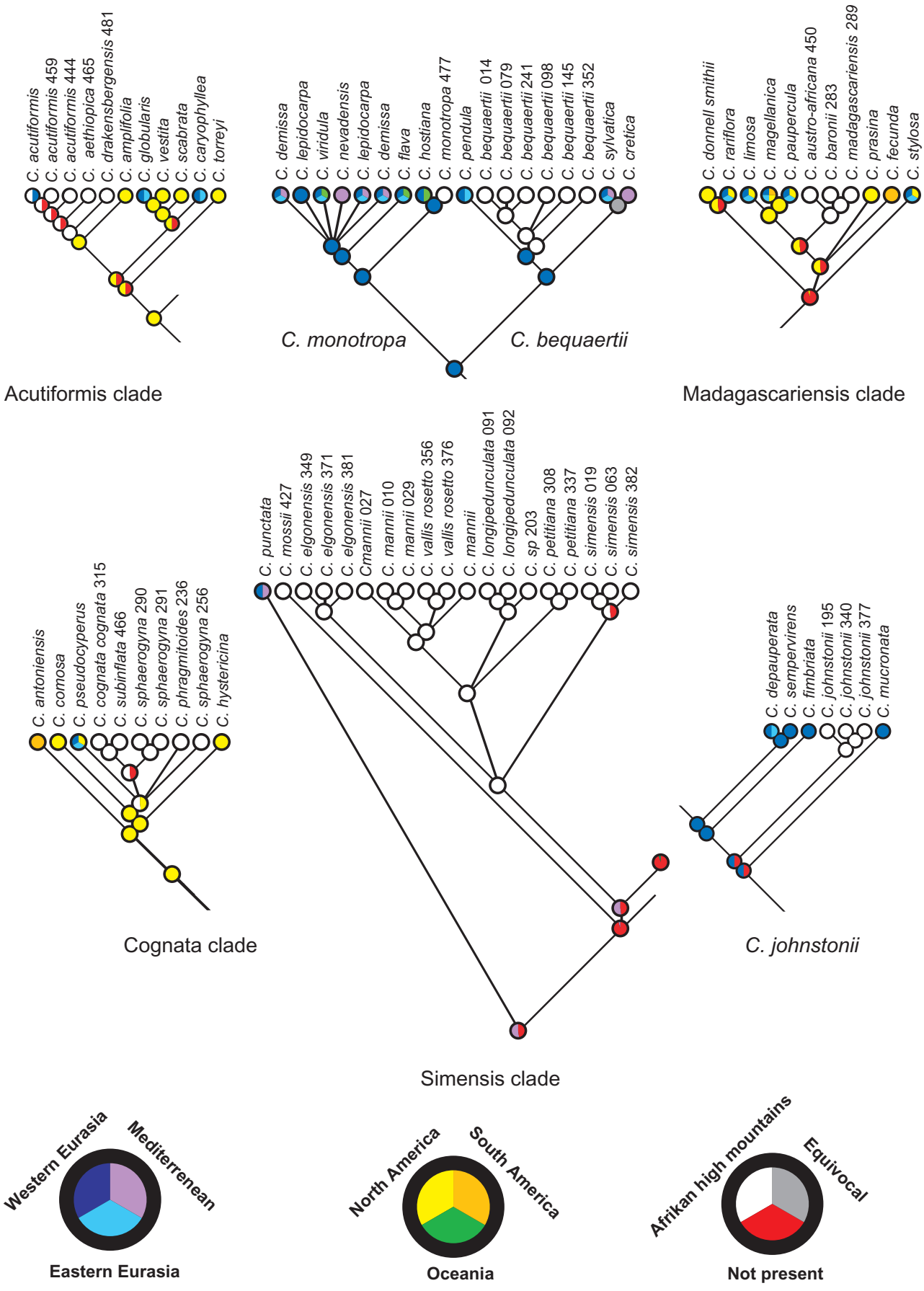


Strict consensus tree of *Carex* subgenus *Vignea* based on the combined nuclear ITS and trnLF dataset reconstructed using parsimony; bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches (only for clades containing accessions from Africa, indicated in bold, African accessions in colour). Where higher support values were achieved in separate analyses of the individual markers, these are given after a slash in bold.

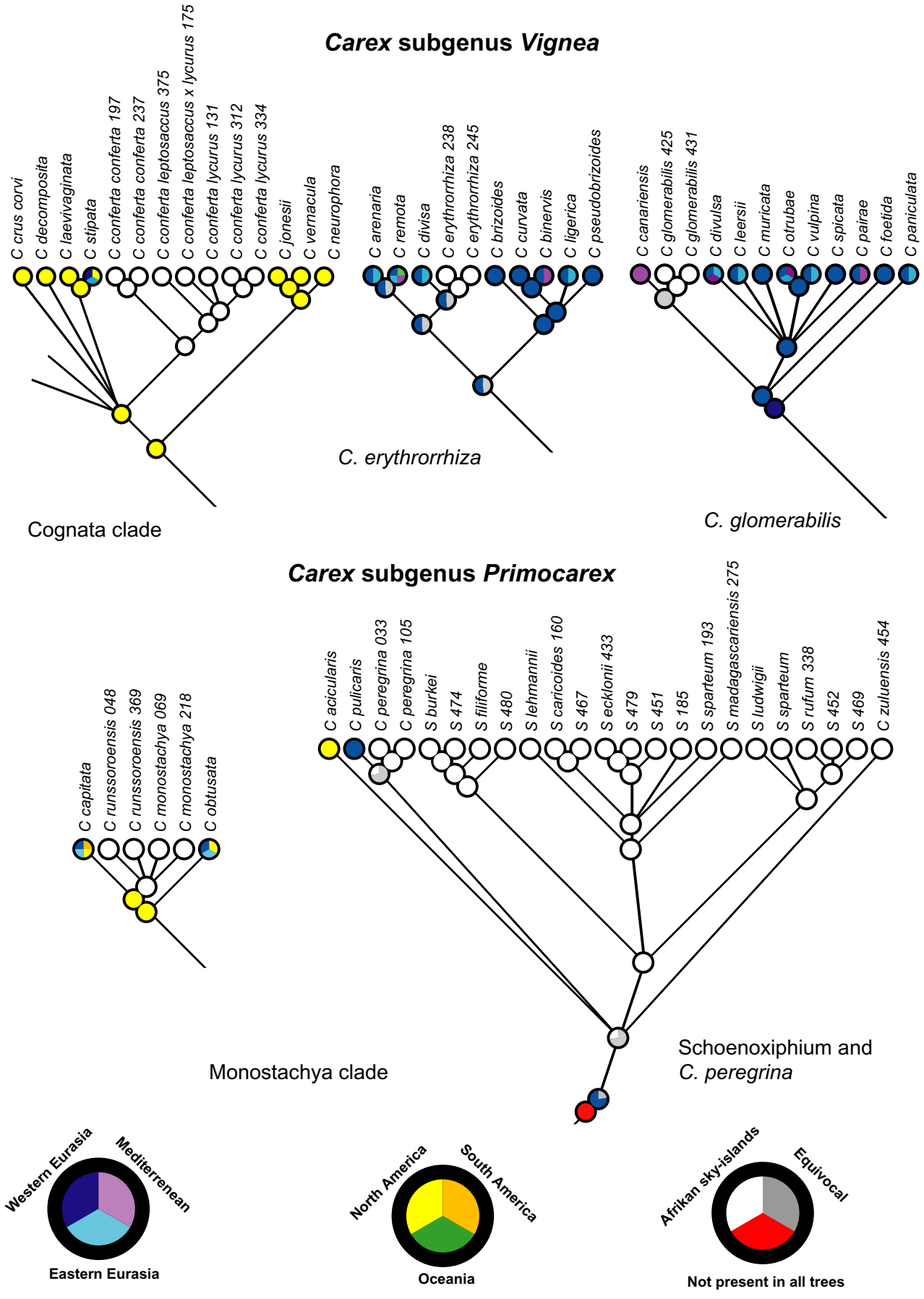
Ranunculus

Strict consensus tree of *Ranunculus* based on the combined nuclear ITS and matK dataset reconstructed using parsimony; bootstrap support values above 50 are given above branches and Bayesian clade credibility values above 0.95 are given below branches (only for clades containing accessions from Africa, indicated in bold, African accessions in colour). Where higher support values were achieved in separate analyses of the individual markers, these are given after a slash in bold.

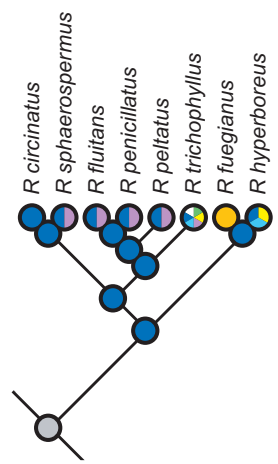
Appendix 6: Ancestral area reconstruction under parsimony; clades in *Carex* subgenus *Carex* containing accessions from the high mountains of Tropical and Southern Africa using the Adams consensus. Colour coded as stated below.



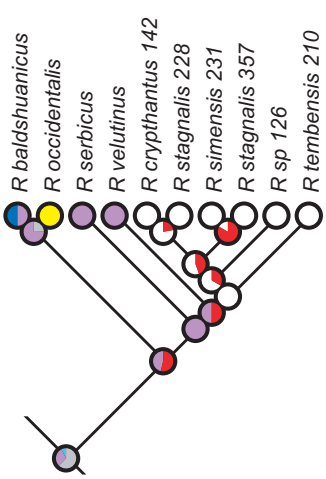
Appendix 6: Ancestral area reconstruction under parsimony; clades in *Carex* subgenus *Primocarex* and *Carex* subgenus *Vignea* containing accessions from the high mountains in Africa using the Adams consensus. Colour coded as stated below.



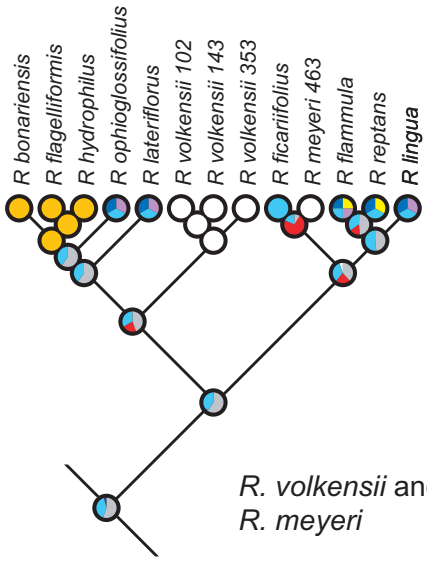
Appendix 6: Ancestral area reconstruction under parsimony; clades in *Ranunculus* containing African accessions using the Adams consensus. Colour coded as stated below.



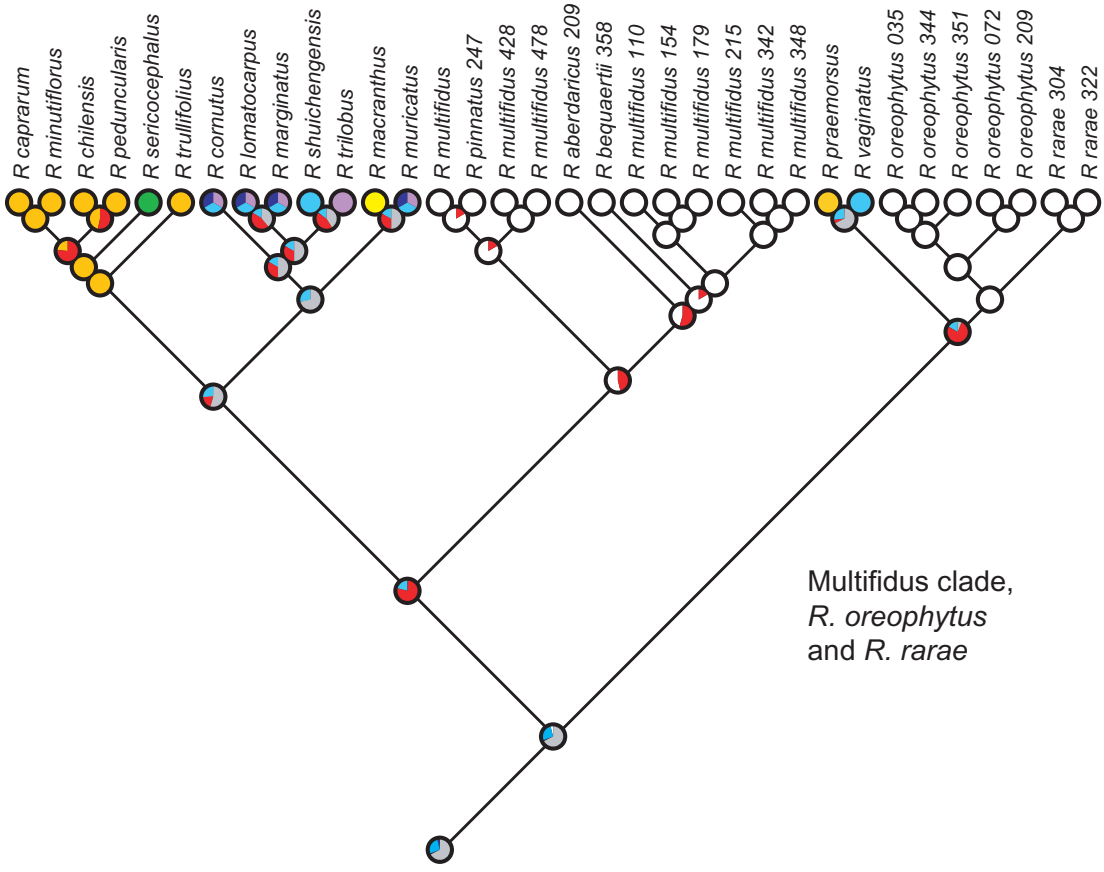
R. tichophyllus



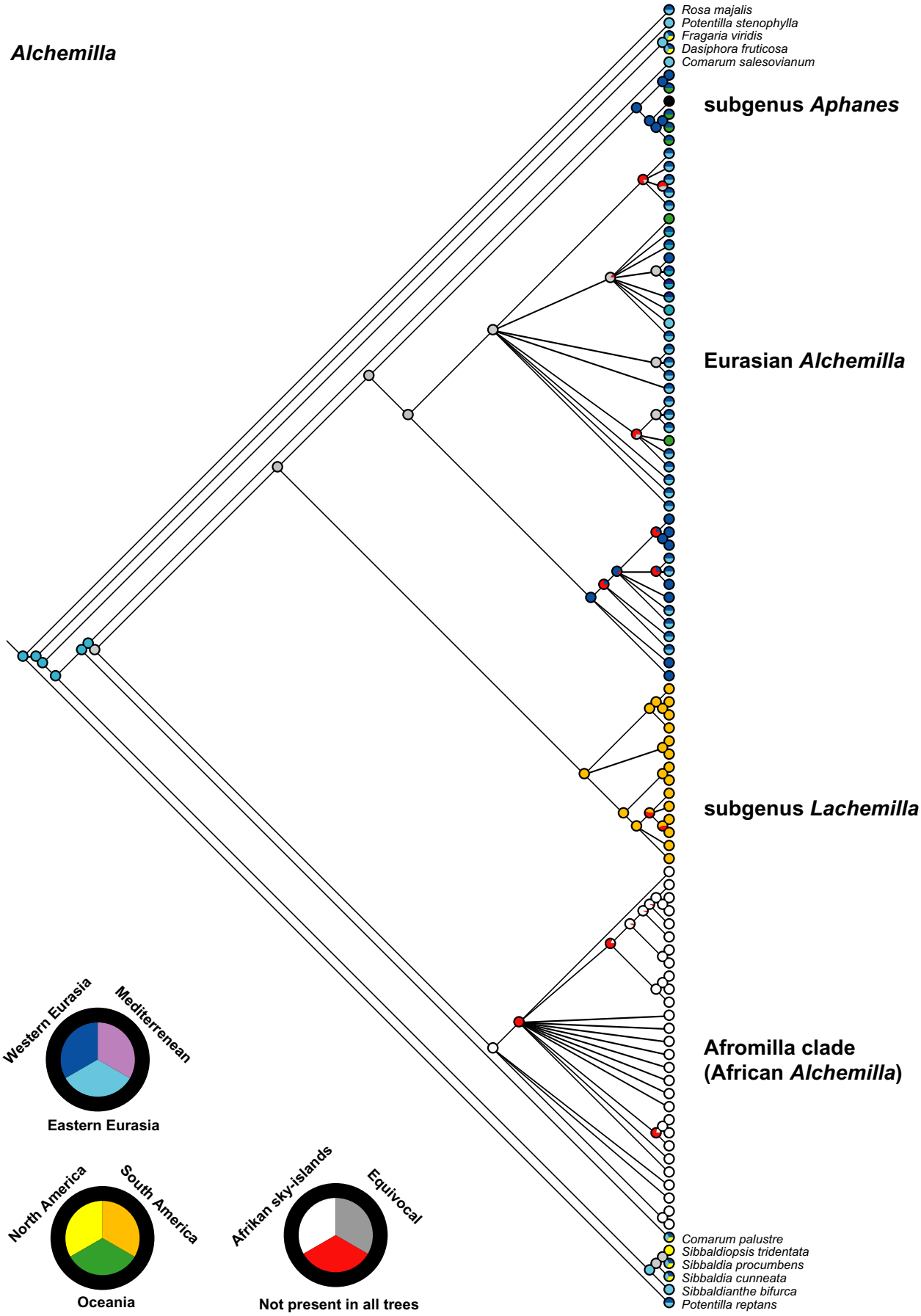
Stagnalis clade



R. volkensii and *R. meyeri*



Multifidus clade, *R. oreophytus* and *R. rarae*



Appendix 6: *Alchemilla* ancestral area reconstruction under parsimony using the Adams consensus. Colour coded as in ledgend.

Appendix 7:

Generalized linear model (GLM) using quasipoisson distribution analysis of *Carex* and *Ranunculus*. Values are shown for most combinations on conservatively estimated clade size (cs estim.) a reduced amount for clade size present in the molecular phylogenetic in the analyses (cs an.) and high estimated clade size (cs high). Disp.= dispersion parameter for quasipoisson family; intercept Sig.= coefficient significance of the intercept as returned by the glm function in R; RD= residual deviance; *Carex*: null deviance on 11 degrees of freedom cs an.=47.3, cs estim.= 56.5, cs high = 84.9; Residual deviance on 10 degrees of freedom; *Ranunculus*: Null deviance on 6 degrees of freedom cs an.= 7.7766, cs estim.= 14.743, cs high = 17.366; Residual deviance on 5 degrees of freedom; cs an.=0.89, cs estim.=1.7 , cs high=1.95. distr. = distribution range; zones = number of altitudinal zones; alt. range = altitudinal range; light= light requirement; water = water availability; hab. hetero.= habitat heterogeneity. Intercept significance value > 0.05 are marked in bold and an asteriks.

	Carex				
	disp.	**inter-cept sig.**	**RD**	**D^2**	**adj. D^2**
conservative estimated clade size					
All factor combined					
age A + distr. + isolation + alt. range + zones + no. hab. + water + light+ hab. hetero.	0.696	0.417	1.406	0.975	0.863
age B + distr. + isolation + alt. range + zones + no. hab. + water avail.+ light+ hab. hetero.	1.369	0.297	2.710	0.952	0.736
age B + distr. + water + zones + x					
age A + distr. + water + zones+ isolation	1.061	0.192	4.55	0.919	0.852
age B + distr. + water + zones+ isolation	0.744	0.057	3.819	0.932	0.876
age A + distr. + water + zones+ alt. range	**0.420**	**0.005***	**2.312**	**0.959**	**0.925**
age B + distr. + water + zones+ alt. range	**0.574**	**0.012***	**3.400**	**0.940**	**0.890**
age A + distr. + water + zones+ no. hab.	0.833	**0.035***	4.028	0.929	0.869
age B + distr. + water + zones+ no. hab.	0.740	**0.023***	3.869	0.932	0.875
age A + distr. + water + zones+ light	1.069	0.057	4.590	0.919	0.925
age B + distr. + water + zones+ light	0.772	**0.028***	3.954	0.930	0.872
age A + distr. + water + zones+ hab. hetero.	0.893	**0.045***	4.154	0.926	0.865
age B + distr. + water + zones+ hab. hetero.	0.731	**0.029***	3.785	0.933	0.877

age + distr. + water + x					
age A + distr. + water + isolation	0.964	0.195	5.067	0.910	0.859
age B + distr. + water + isolation	0.710	**0.050***	4.265	0.925	0.881
age A + distr. + water + alt. range	**0.367**	**0.003***	**2.354**	**0.958**	**0.935**
age B + distr. + water + alt. range	0.661	**0.015***	3.959	0.930	0.890
age A + distr. + water + zones	0.916	**0.038***	4.590	0.919	0.872
age B + distr. + water + zones	**0.499**	**0.006***	**3.413**	**0.940**	**0.905**
age A + distr.+water + no. hab.	0.708	**0.022***	4.168	0.926	0.884
age B + distr. + water + no. hab.	0.648	**0.015***	3.999	0.929	0.889
age A + distr. + water + light	0.950	**0.047***	5.017	0.911	0.935
age B + distr. + water + light	0.706	**0.020***	4.207	0.926	0.883
age A + distr. + water + hab. hetero.	0.788	**0.026***	4.180	0.926	0.884
age B + distr. + water + hab. hetero.	0.630	**0.013***	3.791	0.933	0.895
age + distr. + x					
age A + distr.+ isolation	1.015	0.751	7.170	0.873	0.826
age B+ distr.+ isolation	1.032	0.421	7.7038	0.864	0.813
age A + distr. + zones	1.000	0.092	7.210	0.872	0.825
age B+ distr. + zones	1.029	0.083	6.787	0.880	0.835
age A + distr.+ alt. range	**0.436**	**0.004***	**3.150**	**0.944**	**0.923**
age B+ distr.+ alt. range	0.846	**0.043***	5.811	0.897	0.859
age A + distr.+no. hab. types	0.749	**0.036***	5.927	0.895	0.856
age B+ distr.+no. hab. types	0.813	**0.046***	6.434	0.886	0.843
age A + distr. + water avail	0.850	**0.036***	5.146	0.909	0.875
age B + distr. + water avail.	**0.627**	**0.037***	**4.297**	**0.924**	**0.895**
age A + distr.+light	1.009	0.097	7.465	0.868	0.818
age B+ distr.+light	0.882	**0.045***	6.443	0.886	0.878
age A + distr. + hab. hetero.	0.723	**0.022***	7.210	0.912	0.825
age B.+ distr. + hab. hetero.	0.721	**0.019***	4.995	0.915	0.883
age + zones+ x					
age An+ zones+ isolation	1.000	0.092	7.210	0.872	0.825
age B+ zones+ isolation	1.539	0.265	7.534	0.867	0.817
ageA + zones+ alt. range	2.467	0.940	18.121	0.679	0.560
age B+ zones+ alt. range	1.371	0.063	8.016	0.858	0.827
ageA + distr.+zones	2.467	0.940	18.121	0.679	0.559
age B + distr.+zones	1.026	0.083	6.787	0.880	0.835
ageA + zones+no. hab. types	3.546	0.523	27.318	0.517	0.335
age B+ zones+no. hab. types	1.536	0.094	7.998	0.858	0.805
ageA + zones+water avail.	3.753	0.606	27.820	0.508	0.323
age B + zones+water avail.	**0.952**	**0.027***	**6.679**	**0.882**	**0.838**
ageA + zones+light	2.955	0.189	22.059	0.610	0.463
age B + zones+light	1.543	0.080	7.907	0.860	0.808

ageA + zones+ hab. hetero.	3.209	0.317	24.863	0.560	0.395
age B + zones+ hab. hetero.	1.416	0.066	7.662	0.864	0.814
age + hab. hetero.+ x					
ageA + hab. hetero.+ distr.	**0.723**	**0.022***	**4.995**	**0.912**	**0.878**
age B+ hab. hetero.+ distr.	**0.721**	**0.019***	**4.816**	**0.915**	**0.882**
ageA + hab. hetero.+ isolation	2.470	0.737	17.747	0.686	0.568
age B+ hab. hetero.+ isolation	1.327	0.221	7.554	0.866	0.816
ageA + hab. hetero.+alt. range	2.714	0.192	21.504	0.620	0.477
age B+ hab. hetero.+alt. range	1.416	0.066	7.663	0.864	0.814
ageA + hab. hetero.+ zones	3.209	0.317	24.863	0.560	0.395
age B+ hab. hetero.+ zones	1.350	0.060	7.545	0.867	0.816
ageA + hab. hetero.+ no. hab. types	3.235	0.282	23.978	0.576	0.417
age B+ hab. hetero.+ no. hab. types	1.094	**0.033***	6.390	0.887	0.845
ageA + hab. hetero.+ water avail.	2.983	0.209	22.910	0.595	0.443
age B+ hab. hetero.+ water avail.	1.081	0.054	8.218	0.855	0.800
ageA + hab. hetero.+ light	2.920	0.277	23.30	0.588	0.433
age B + hab. hetero.+ light	1.196	**0.050***	7.878	0.861	0.808
age + x					
age A + distr.	1.047	0.122	8.401	0.851	0.818
age B+ distr.	0.935	0.087	8.254	0.854	0.822
age A + isolation	2.590	0.146	22.353	0.605	0.517
age B + isolation	1.392	0.596	9.889	0.825	0.786
age A + alt. range	2.522	0.215	22.647	0.599	0.510
age B + alt. range	1.317	0.070	8.310	0.853	0.820
age A + zones	3.380	0.575	0.507	0.397	0.397
age B + zones	1.371	0.063	8.016	0.858	0.827
age A + no. hab. types	3.934	0.974	30.560	0.459	0.339
age B + no. hab. types	1.519	0.203	11.482	0.797	0.752
age A + water avail.	26.735	0.378	26.735	0.527	0.422
age B + water avail.	0.991	0.056	9.321	0.835	0.800
age A + light	4.255	0.989	31.038	0.451	0.329
age B + light	1.457	0.133	10.779	0.809	0.767
age A + hab. hetero.	2.853	0.286	56.523	0.559	0.461
age B + hab. hetero.	1.154	**0.050***	8.443	0.851	0.817
distr. + water + x					
distr. + water + ageBAyout	0.850	**0.036***	5.146	0.909	0.895
distr. + water + ageBAyout	0.850	**0.036***	5.146	0.909	0.895
distr. + water + isolation	0.627	**0.012***	4.297	0.924	0.823
distr. + water + alt. range	1.197	0.063	7.260	0.872	0.824
distr. + water + zones	1.225	**0.050***	7.363	0.870	0.821
distr. + water + no. hab. types	1.114	**0.032***	7.241	0.872	0.824

distr. + water + light	1.162	**0.033***	6.858	0.879	0.833
distr. + water + hab. hetero.	1.167	**0.031***	7.005	0.876	0.830
distr.+water +x (all possibly combinations)		>0.1			
distr. + no. hab. types + x (all possibly combinations)		>0.1			
distr. + x					
distr.+ isolation	1.786	0.925	15.369	0.728	0.668
distr.+ alt. range	1.569	0.256	14.109	0.750	0.695
distr.+ zones	1.755	0.633	15.782	0.721	0.659
distr.+ no. hab. types	0.834	**0.026***	7.393	0.869	0.840
distr.+ water avail.	1.119	**0.030***	7.466	0.868	0.839
distr.+ light	1.312	0.116	11.285	0.800	0.756
distr.+ hab. hetero.	1.287	0.074	10.398	0.816	0.775
Single factors					
age A	**4.086**	**0.027***	**31.296**	**0.446**	**0.391**
age B	**1.373**	**0.000***	**11.507**	**0.796**	**0.776**
distr.	**1.581**	**0.000***	**15.783**	**0.721**	**0.693**
isolation	6.889	0.573	54.130	0.042	0.055
alt. range	7.379	0.323	48.578	0.141	0.000
zones	8.129	0.800	55.989	0.009	0.055
no. hab. types	4.603	0.075	38.219	0.324	0.256
water avail.	4.034	0.072	38.048	0.327	0.260
light	6.125	0.359	50.784	0.102	0.012
hab. hetero.	5.120	0.083	37.674	0.333	0.267
Clade size in analysis					
age A + distr. + isolation + alt. range + zones+ no. hab.+ water avail.+ light+ hab. hetero.	0.945	0.519	1.913	0.960	0.777
age B + distr. + isolation + alt. range + zones+ no. hab.+ water avail.+ light+ hab. hetero.	1.814	0.351	1.814	0.924	0.582
age A + distr. + water + zones+ alt. range	*0.528*	***0.016****	*3.036*	*0.936*	*0.882*
age A + distr. + water + zones	0.928	0.062	4.799	0.899	0.841
age A + distr. + water + alt. range	**0.458**	**0.009***	**3.057**	**0.935**	**0.899**
age A + distr. + water + hab. hetero.	0.845	**0.049***	4.641	0.902	0.846
age A+ distr.+water avail.	0.844	**0.050***	5.228	0.890	0.848
age B. + distr. + water + zones+ alt. range	*0.777*	***0.036****	*4.585*	*0.903*	*0.822*
age B + distr. + water + zones	0.801	**0.036***	4.948	0.895	0.836
age B + distr. + water + alt. range	**0.677**	**0.023***	**4.604**	**0.903**	**0.847**
age B + distr. + water + hab. hetero.	0.780	**0.032***	4.848	0.898	0.839
age A + distr.+water avail.	0.844	**0.058**	5.227	0.890	0.848

age B+ distr.+water avail.	0.722	**0.026***	5.098	0.892	0.852
age A + distr.+ zones	0.923	0.100	6.497	0.863	0.811
age B+ distr.+ zones	1.047	0.121	7.258	0.847	0.789
age A + distr.+ alt. range	***0.474***	***0.009****	***3.562***	***0.925***	***0.897***
age B+ distr.+ alt. range	0.911	0.077	6.571	0.861	0.809
age A+ distr.+ hab. hetero.	0.758	**0.042***	5.241	0.889	0.847
age B+ distr.+ hab. hetero.	0.840	**0.041***	5.815	0.877	0.831
age A+ distr.	0.903	0.097	7.276	0.846	0.812
age B+ distr.	0.904	0.091	8.062	0.830	0.792
age A	3.038	**0.018***	24.879	0.474	0.422
age B	1.221	**0.001***	10.636	0.775	0.753
distr.	1.475	**0.001***	14.443	0.695	0.664
High estimated cladesize					
age A + distr. + isolation + alt. range + zones+ no. hab.+ water avail.+ light+ hab. hetero.	0.474	0.379	0.932	0.989	0.940
age B + distr. + isolation + alt. range + zones+ no. hab.+ water avail.+ light+ hab. hetero.	1.622	0.256	3.128	0.963	0.797
age A + distr. + water + zones+ alt. range	***0.497***	***0.005****	***2.966***	***0.965***	***0.936***
age A+ distr.+water + zones	1.322	0.059	6.563	0.923	0.879
age A + distr. + water + alt. range	**0.435**	**0.002***	**3.002**	**0.965**	**0.944**
age A+ distr.+water + hab. hetero.	1.186	**0.048***	6.407	0.925	0.881
age B. + distr. + water + zones+ alt. range	***0.842***	***0.019***	***4.950***	***0.942***	***0.893***
age B+ distr.+water + zones	1.318	**0.020***	5.554	0.935	0.897
age B + distr. + water + alt. range	**0.721**	**0.011***	**4.950**	**0.942**	**0.908**
age B + distr. + water + hab. hetero.	0.904	**0.021***	5.658	0.933	0.895
age A+ distr.+water avail.	1.217	0.061	7.483	0.912	0.879
age B+ distr.+water avail.	0.876	0.019*	6.117	0.928	0.901
age A + distr.+ zones	1.391	0.132	9.645	0.886	0.844
age B+ distr.+ zones	1.195	0.084	8.521	0.900	0.862
age A + distr.+ alt. range	0.486	**0.003***	3.705	0.956	0.940
age B+ distr.+ alt. range	1.090	**0.050***	7.703	0.909	0.875
age A+ distr.+ hab. hetero.	1.085	**0.046***	7.424	0.913	0.880
age B+ distr.+ hab. hetero.	0.909	**0.027***	6.905	0.919	0.888
age A+ distr.	1.408	0.200	11.293	0.867	0.837
age B+ distr.	1.190	0.109	10.901	0.872	0.843
age A	5.184	**0.013***	41.064	0.516	0.468
age B	1.503	**<0.001***	13.627	0.839	0.823
distr.	2.627	**0.001***	26.058	0.693	0.662

Ranunculus

	Disp.	Intercept Sig.	RD	D^2	Adj. D^2
conservative estimated clade size					
age A + distr. + isolation + alt. range + zones + no. hab. + water + light+ hab. hetero.	NA	NA	-	NA	NA
age B + distr. + isolation + alt. range + zones + no. hab. + water avail.+ light+ hab. hetero.	NA	NA	-	NA	NA
age + distr. + water + zones+ alt. range					
age A + distr. + water + zones+ alt. range	0.147	0.317	0.154	0.990	0.937
age B. + distr. + water + zones+ alt. range	0.017	0.561	0.017	0.999	0.993
age + distr. + water + x					
age A + distr. + water + zones	0.085	0.147	0.177	0.988	0.964
age B + distr. + water + zones	0.014	0.740	0.028	0.998	0.994
age A + distr. + water + alt. range	0.088	0.137	0.184	0.988	0.963
age B + distr. + water + alt. range	0.018	0.858	0.035	0.998	0.993
age A + distr. + water + light	0.087	0.122	0.182	0.988	0.963
age B + distr. + water + light	0.018	0.825	0.035	0.998	0.993
age A + distr. + water + hab. hetero.	0.082	0.190	0.169	0.989	0.967
age B + distr. + water + hab. hetero.	0.018	0.911	0.036	0.992	0.993
age + distr. + x					
age A. + distr. + alt. range	0.418	0.522	1.267	0.914	0.828
age B + distr. + alt. range	0.310	0.930	0.890	0.940	0.879
age A + distr. + zones	0.411	0.306	1.318	0.911	0.821
age B + distr. + zones	0.396	0.795	1.218	0.917	0.835
age A + distr. + light	0.443	0.468	1.366	0.907	0.815
age B + distr. + light	0.352	0.926	1.028	0.930	0.861
age A + distr. + water avail.	**0.059**	**0.029***	**0.184**	**0.988**	**0.975**
age B + distr. + water avail.	**0.013**	**0.556**	**0.038**	**0.997**	**0.995**
age A+distr. + hab. hetero.	0.473	0.588	1.440	0.902	0.805
age B + distr. + hab. hetero.	0.378	0.963	1.091	0.926	0.852
distr. + zones+ No. Hab. types + x					
distr. + zones+ no. hab. types + isolation	0.192	0.776	0.422	0.971	0.914
distr. + zones+ no. hab. types + alt. range	0.185	0.135	0.378	0.974	0.923
distr. + zones+ no. hab. types + Light requirm.	0.218	0.150	0.472	0.968	0.904

distr. + zones+ no. hab. types + water avail.	0.242	0.125	0.501	0.966	0.898
distr. + zones+ no. hab. types + hab. hetero.	0.161	0.081	0.308	0.979	0.937
distr. + zones+ x					
distr. + zones+ no. hab. types	**0.160**	**0.021***	**0.503**	**0.932**	**0.966**
distr. + zones+ alt. range	0.154	0.107	0.311	0.979	0.939
distr. + zones+ water avail.	0.269	0.063	0.739	0.950	0.900
distr. + zones+ hab. hetero.	0.229	0.060	0.601	0.959	0.918
distr. + water + x					
distr.+ water + zones+ alt. range	0.154	0.107	0.311	0.979	0.937
distr.+ water + alt. range	0.553	0.269	1.764	0.880	0.761
distr.+ water + zones	0.269	0.063	0.739	0.950	0.900
distr.+ water + hab. hetero.	0.484	0.159	1.350	0.908	0.817
distr. + x					
distr.+ isolation	0.329	0.309	1.421	0.904	0.855
distr.+ alt. range	0.417	0.064	1.818	0.877	0.815
distr.+ zones	0.309	**0.043***	1.322	0.910	0.865
distr.+ no. hab. types	0.405	0.060	1.734	0.882	0.826
distr.+ water avail.	0.416	0.112	1.797	0.878	0.817
distr.+ light	0.417	0.081	1.812	0.877	0.816
distr.+ hab. hetero.	0.386	0.053	1.700	0.885	0.827
age + x					
age A + distr.	0.352	0.252	1.485	0.899	0.849
age B+ distr.	0.298	0.614	1.218	0.917	0.876
age A + isolation	1.750	0.548	6.052	0.589	0.384
age B + isolation	3.060	0.125	9.985	0.323	0.000
age A + alt. range	1.486	0.417	5.562	0.623	0.434
age B + alt. range	0.618	0.069	2.741	0.814	0.721
age A + zones	1.082	0.409	4.058	0.725	0.587
age B + zones	0.497	0.091	1.852	0.874	0.816
age A + no. hab. types	1.531	0.932	4.673	0.683	0.525
age B + no. hab. types	0.409	0.164	1.451	0.902	0.852
age A + water avail.	0.162	0.091	0.687	0.953v	0.930
age B + water avail.	0.118	0.427	0.478	0.968	0.951
age A + light	3.604	0.819	11.925	0.191	0.000
age B + light	2.713	0.364	8.644	0.414	0.121
age A + hab. hetero.	1.821	0.242	6.612	0.552	0.327
age B + hab. hetero.	0.745	**0.036***	3.215	0.782	0.673
Single factors					

age A	3.377	0.494	14.710	0.002	0.000
age B	2.207	0.072	10.498	0.288	0.146
distr.	0.333	0.035*	1.818	0.877	0.852
isolation	2.630	0.065	10.092	0.315	0.179
alt. range	1.956	0.882	7.473	0.493	0.392
zones	1.689	0.624	7.598	0.485	0.382
no. hab. types	2.177	0.524	8.919	0.395	0.274
light	2.726	0.970	12.202	0.172	0.007
water	0.451	**0.034***	2.198	0.851	0.821
hab. hetero.	2.468	0.783	9.325	0.367	0.241
Clade size in analysis					
age A + distr. + isolation + alt. range + zones + no. hab. + water + light+ hab. hetero.	NA	NA	-	NA	NA
age B + distr. + isolation + alt. range + zones + no. hab. + water avail.+ light+ hab. hetero.	NA	NA	-	NA	NA
age A + distr. + water + zones	0.043	0.116	0.089	0.989	0.966
age B + distr. + water + zones	0.014	0.997	0. 027	0.996	0.989
age A + distr. + water + alt. range	0.050	0.126	0.104	0.987	0.960
age B + distr. + water + alt. range	0.012	0.971	0.024	0.997	0.991
age A+ distr.+ alt. range	0.269	0.557	0.824	0.894	0.788
age A+ distr.+ zones	0.221	0.274	0.693	0.911	0.821
age A+ distr.+no. hab. types	0.173	0.333	0.560	0.928	0.856
age A+ distr.+water avail.	**0.037**	**0.044***	**0.115**	**0.985**	**0.971**
age B.+ distr.+water avail.	**0.010**	**0.002***	**0.028**	**0.996**	**0.993**
age A+ distr.+ hab. hetero.	0.284	0.558	0.886	0.886	0.772
age A+ distr.	0.213	0.344	0.887	0.901	0.802
distr.+ water + hab. hetero.	0.284	0.156	0.841	0.784	0.892
distr. + zones+ no. hab. types	0.091	0.021*	0.284	0.964	0.927
age A	1.772	0.879	4.305	0.446	0.336
age B	1.082	0.069	5.336	0.357	0.228
distr.	0.219	**0.043***	1.180	0.199	0.038
water.	0.292	**0.042***	1.428	0.816	0.780
High estimated cladesize					
age A + distr. + isolation + alt. range + zones + no. hab. + water + light+ hab. hetero.	NA	NA	-	NA	NA
age B + distr. + isolation + alt. range + zones + no. hab. + water avail.+ light+ hab. hetero.	NA	NA	-	NA	NA

age + distr. + water + zones+ alt. range					
age A + distr. + water + zones+ alt. range	0.043	0.187	0.044	0.997	0.985
age B. + distr. + water + zones+ alt. range	0.001	0.180	0.001	0.999	0.999
age + distr. + water + x					
age A + distr. + water + zones	0.025	0.050*	0.050	0.997	0.991
age B + distr. + water + zones	**0.001**	**0.024***	**0.002**	**1.0**	**1.0**
age A + distr. + water + alt. range	0.024	0.039*	0.049	0.997	0.992
age B + distr. + water + alt. range	0.003	0.018	0.006	1.0	0.999
age B + distr. + water + light	0.003	0.034	0.007	1.0	1.0
age A + distr. + water + light	0.025	0.034	0.050	0.997	0.991
age A + distr. + water + hab. hetero.	**0.019**	**0.048***	**0.038**	**0.998**	**0.993**
age B + distr. + water + hab. hetero.	0.003	0.026	0.005	1.0	0.999
age + distr. + x					
age A + distr. + alt. range	0.079	0.092	0.240	0.986	0.972
age B + distr. + alt. range	0.052	0.230	0.154	0.991	0.982
age A + distr. + zones	0.418	0.525	1.267	0.914	0.828
age B + distr. + zones	0.310	0.930	0.890	0.940	0.879
age A + distr. + light	0.090	0.087	0.273	0.984	0.969
age B + distr. + light	0.067	0.205	0.201	0.988	0.977
age A + distr. + water avail.	0.059	0.029*	0.184	0.988	0.975
age B + distr. + water avail.	0.013	0.001*	0.038	0.997	0.995
age A + distr. + hab. hetero.	0.473	0.588	1.440	0.902	0.805
age B + distr. + hab. hetero.	0.378	0.963	1.091	0.926	0.852
distr. + water + x					
distr.+ water + hab. hetero.	0.095	**0.039**	0.277	0.984	0.968
age B+ distr.	0.081	**0.024**	0.332	0.981	0.971
Single fators					
age A	3.866	0.918	17.320	0.003	0.001
age B	2.870	0.315	13.853	0.202	0.043
distr.	0.070	**<0.001**	0.358	0.979	0.975
water	0.183	**<0.001**	0.853	0.951	0.941

Appendix 8:

Kendall's rank correlation tau of predictor variables

Significant p values (p<0.05) are indicated in bold. Bonferroni probabilities are denoted by asterisks (*=p>0.05; **=p>0.01; ***p>0.001).

Carex: **Kendall's rank correlation tau of predictor variables**

	Heterogen.	**Water**	**Light**	**No. habitats**	**Alt. zones**	**Alt. range**	**Isolation**	**Distributio n**
Age	z=1.530 p=0.126 tau=0.349	z=0.489 p=0.625 tau=0.127	z=0.798 p=0.425 tau=0.193	z=1.827 p=0.068 tau=0.442	z=-0.367 p=0.714 tau=-0.093	z=1.090 p=0.276 tau=0.267	z=1.324 p=0.186 tau=0.321	z=0.711 p=0.477 tau=0.167
Distributi on	z=1.572 p=0.116 tau=0.373	z=0.667 p=0.505 tau=0.181	z=0.818 p=0.413 tau=0.206	z=1.349 p=0.177 tau=0.340	z=1.316 p=0.188 tau=0.347	z=1.038 p=0.300 tau=0.265	z=0.226 p=0.821 tau=0.057	--
Isolation	z=-0.074 p=0.941 tau=-0.018	z=-0.602 p=0.547 tau=-0.169	z=-0.922 p=0.357 tau=-0.240	z=0.619 p=0.536 tau=0.162	z=-0.485 p=0.628 tau=-0.133	z=-0.082 p=0.934 tau=-0.022	--	--
Alt. range	**z=2.188** **p=0.029*** **tau=0.542**	z=0.546 p=0.585 tau=0.155	z=1.462 p=0.144 tau=0.384	**z=2.129** **p=0.033*** **tau=0.561**	z=1.333 p=0.183 tau=0.368	--	--	--
Alt. zones	z=1.750 p=0.080 tau=0.448	z=-0.214 p=0.831 tau=-0.063	z=0.861 p=0.390 tau=0.234	z=0.578 p=0.563 tau=0.158	--	--	--	--
No. habitats	**z=2.789** **p=0.005**** **tau=0.683**	z=0.598 p=0.550 tau=0.167	**z=1.985** **p=0.047*** **tau=0.515**	--	--	--	--	--
Light	**z=2.840** **p=0.005**** **tau=0.694**	z=0.594 p=0.553 tau=0.166	--	--	--	--	--	--
Water	z=1.145 p=0.252 tau=0.301	--	--	--	--	--	--	--

Ranunculus: Kendall's rank correlation tau of predictor variables

	Heterogen.	**Water**	**Light**	**No. habitats**	**Alt. zones**	**Alt. range**	**Isolation**	**Distribution**
Age	z=1.283 p=0.199 tau=0.434	z=0.932 p=0.351 tau=0.308	z=0.858 p=0.391 tau=0.299	z=0.858 p=0.391 tau=0.299	z=0.963 p=0.336 tau=0.325	z=0.172 p=0.864 tau=0.060	z=1.728 p=0.084 tau=0.607	z=0.487 p=0.626 tau=0.168
Distribution	**z=2.198** **p=0.0279*** **tau=0.788**	**z=2.625** **p=0.009**** **tau=0.917**	z=1.443 p=0.149 tau=0.535	z=1.082 p=0.279 tau=0.401	**z=2.367** **p=0.018*** **tau=0.849**	**z=2.164** **p=0.030*** **tau=0.802**	z=-0.403 p=0.687 tau=-0.151	--
Isolation	z=0.146 p=0.690 tau=0.399	z=0.194 p=0.846 tau=0.069	z=0 p=1 tau=0	z=0.638 p=0.523 tau=0.242	z=0.399 p=0.690 tau=0.146	z=-0.213 p=0.832 tau=-0.081	--	--
Alt. range	z=1.784 p=0.074 tau=0.648	**z=2.252** **p=0.024*** **tau=0.797**	z=0.380 p=0.704 tau=0.143	z=1.902 p=0.057 tau=0.714	**z=2.141** **p=0.032*** **tau=0.778**	--	--	--
Alt. zones	**z=2.508** **p=0.012*** **tau=0.882**	**z=2.594** **p=0.009**** **tau=0.890**	z=1.249 p=0.212 tau=0.454	z=1.249 p=0.212 tau=0.454	--	--	--	--
No. habitats	z=0.714 p=0.475 tau=0.259	z=1.559 p=0.119 tau=0.552	z=0 p=1 tau=0	--	--	--	--	--
Light	z=1.249 p=0.212 tau=0.454	z=1.559 p=0.119 tau=0.552	--	--	--	--	--	--
Water	**z=2.270** **p=0.023*** **tau=0.779**	--	--	--	--	--	--	--

Appendix 9:

List of all taxa used in alayses including authors, voucher information and GenBank accession numbers. Authors of sections and subsections: *Alchemilla* sect. Longicaules Rothm.; *Alchemilla* sect. Schizophyllae (Rothm.) Notov; *Alchemilla* sect. Parvifoliae Rothm.; *Alchemilla* sect. Subcuneatifoliae (De Wild.) Rothm.; *Alchemilla* sect. Grandifoliae Rothm.; *Alchemilla* sect. Geraniifoliae (Haum. & Balle) Rothm.; *Alchemilla* sect. Pedatae (Rothm.) Notov; *Alchemilla* sect. Alpinae Buser ex Camus; *Alchemilla* sect. Alpinae ser. Hoppeanae Buser ex Rothm.; *Alchemilla* sect. Alpinae ser. Saxatiles Buser ex Rothm.; *Alchemilla* sect. Splendentes Buser; *Alchemilla* sect. Plicatae S.E.Fröhner; *Alchemilla* sect. Coriaceae S.E.Fröhner, *Alchemilla* sect. Decumbentes S.E.Fröhner; *Alchemilla* sect. Erectae S.E.Fröhner; *Alchemilla* sect. Flabellatae S.E.Fröhner; *Alchemilla* sect. Calycinae Buser; *Alchemilla* sect. Glaciales S.E.Fröhner; *Alchemilla* sect. Ultravulgares S.E.Fröhner; *Alchemilla* sect. Calycinae Buser; *Alchemilla* sect. Villosae Rothm; *Alchemilla* sect. Pubescentes Buser; *Alchemilla* sect. Pentaphylleae Buser ex Camus; Aphanes sect. Quadridentatae Rothm. [1] = genus type; [2] = section type

***genus species* author**	**section**	**voucher: collector / no. (herbarium)**	**trnLF**	**ITS**
African *Alchemilla* species				
A. abyssinica Fres.	sect. Longicaules	Gehrke / BG-Af 225 (ZH)	-	EU072507
A. andringitrensis R. Viguier & De Wild.	sect. Schizophyllae	Gehrke / BG-Af 292 (ZH)	EU072595	EU072509
A. argyrophylla Oliv.	sect. Parvifoliae	Gehrke / BG-Af 016 (ZH)	EU072599	EU072512
A. colura Hill.	sect. Longicaules	Gehrke / BG-Af 464 (ZH)	EU072604	EU072517
A. cryptantha Steud. ex A. Rich.	sect. Longicaules	Gehrke / BG-Af 248 (ZH)	EU072607	EU072520
A. dewildermanii T.C.E.Fr.	sect. Subcuneatifoliae	Gehrke / BG-Af 066 (ZH)	EU072609	EU072522
A. ellenbeckii Engl.	sect. Longicaules	Gehrke / BG-Af 104 (ZH)	EU072610	EU072523
A. elongata Eckl. & Zeyher	sect. Longicaules	Gehrke / BG-Af 446 (ZH)	EU072611	EU072524
A. elongensis Mildbr.	sect. Subcuneatifoliae	Gehrke / BG-Af 140 (ZH)	EU072612	EU072525
A. fischeri Engl.	sect. Longicaules	Gehrke / BG-Af 205 (ZH)	-	EU072529
A. gracilipes (Engl.) Engl.	sect. Longicaules	Gehrke / BG- Af 127 (ZH)	EU072620	EU072532
A. granvikii T.C.E.Fr.	sect. Longicaules	Gehrke / BG-Af 023 (ZH)	EU072621	EU072533
A. hageniae T.C.E.Fr.	sect. Grandifoliae	Gehrke / BG-Af 005 (ZH)	EU072623	EU072535
A. haumanii Engl.	sect. Grandifoliae	Gehrke / BG-Af 204 (ZH)	EU072624	EU072536
A. hildebrandtii Engl.	sect. Schizophyllae	Gehrke / BG-Af 258 (ZH)	EU072626	EU072538
A. johnstonii Oliv.	sect. Geraniifoliae	Gehrke / BG-Af 364 (ZH)	EU072632	EU072544
A. kiwuensis Engl.	sect. Longicaules	Gehrke / BG-Af 223 (ZH)	EU072633	EU072545
A. microbetula T.C.E.Fr.[2]	sect. Parvifoliae	Gehrke / BG-Af 360 (ZH)	EU072636	EU072548
A. pedata Hochst. ex A. Rich.	sect. Pedatae	Gehrke / BG-Af 214 (ZH)	EU072642	EU072553
A. roccatii Cort.	sect. Geraniifoliae	Gehrke / BG-Af 365 (ZH)	-	EU072557
A. rutenbergii O. Hoffm.	sect. Schizophyllae	Gehrke / BG-Af 253 (ZH)	-	EU072558
A. schizophylla Bak.	sect. Schizophyllae	Gehrke / BG-Af 282 (ZH)	EU072646	EU072560
A. stuhlmanii Engl.	sect. Subcuneatifoliae	Gehrke / BG-Af 363 (ZH)	EU072649	EU072564
A. subnivalis Bak.	sect. Subcuneatifoliae	Gehrke / BG-Af 362 (ZH)	EU072650	EU072565
A. x subnivalis	sect. Subcuneatifoliae	Gehrke / BG-Af 36 (ZH)	EU072659	EU072575
A. triphylla Rothm.	sect. Subcuneatifoliae	Gehrke / BG-Af 361 (ZH)	EU072655	EU072570
A. volkensii Engl.	sect. Longicaules	Gehrke / BG-Af 205 (ZH)	-	EU072572
A. woodii Kuntze	sect. Longicaules	Gehrke / BG-Af 453 (ZH)	EU072658	EU072574

Eurasian *Alchemilla* species

A. aff. retinervis Buser	unknown	Frost-Olsen / 5690 (ZH)	EU072594	EU072556
A. alpina L.	sect. Alpinae ser. Saxatiles	Gehrke / BG-E 392 (ZH)	EU072595	EU072508
A. angustata S.E.Fröhner	sect. Alchemilla	Gehrke / BG-E 403 (ZH)	EU072597	EU072510
A. aranica S.E.Fröhner	sect. Splendentes	Frost-Olsen / 7713 (ZH)	EU072598	EU072511
A. atriuscula S.E.Fröhner	sect. Alpinae ser. Hoppeanae	Frost-Olsen / 12776 (ZH)	EU072600	EU072513
A. catachnoa Rothm.	sect. Alchemilla	Frost-Olsen / 389 (ZH)	EU072601	EU072514
A. charbonelliana Buser	sect. Alpinae ser. Hoppeanae	Frost-Olsen / 12908 (ZH)	EU072602	EU072515
A. colorata Buser	sect. Plicatae	Frost-Olsen / 8986 (ZH)	EU072603	EU072516
A. coriacea Buser	sect. Coriaceae	Frost-Olsen / 10872 (ZH)	EU072605	EU072518
A. crinita Buser	sect. Alchemilla	Gehrke / BG-E 390 (ZH)	EU072606	EU072519
A. decumbens Buser[2]	sect. Decumbentes	Frost-Olsen / 8592 (ZH)	EU072608	EU072521
A. epipsila Buser[2]	sect. Erectae	Frost-Olsen / 251 (ZH)	EU072613	EU072526
A. exigua Buser ex Paulin	sect. Plicatae	Lippert / 417 (ZH)	EU072614	-
A. faeroensis (Lange) Buser	possibly sect. Splendentes	Frost-Olsen / 2000-BI-00121 (ZH)	EU072615	EU072527
A. fallax Buser	sect. Flabellatae	Frost-Olsen / 7705A (ZH)	EU072616	EU072528
A. filicaulis Huds.	sect. Plicatae	Gehrke / BG-E 386 (ZH)	EU072637	EU072549
A. fissa Hegetschw.[2]	sect. Calycinae	Gehrke / BG-E 395 (ZH)	EU072617	EU072539
A. flabellata Buser[2]	sect. Flabellatae	Frost-Olsen / 11859 (ZH)	EU072618	EU072531
A. sp. sect. glacalis Buser	sect. Glaciales	Frost-Olsen / 11699 (ZH)	EU072619	EU072562
A. grenieri Guillot	sect. Alpinae ser. Saxatiles	Frost-Olsen / 12695 (ZH)	EU072622	EU072534
A. heptagona Juz.[2]	sect. Ultravulgares	Frost-Olsen / 6999 (ZH)	EU072625	EU072537
A. hispanica S.E.Fröhner	sect. Splendentes	Frost-Olsen / 9065 (ZH)	EU072627	EU072539
A. ilerdensis S.E.Fröhner	sect. Alchemilla	Gehrke / BG-E 409 (ZH)	EU072628	EU072540
A. incisa Buser	sect. Coriaceae	Gehrke / BG-E 399 (ZH)	EU072629	EU072541
A. indivisa (Buser) Rothm.	sect. Erectae	Frost-Olsen / 3383 (ZH)	EU072630	EU072542
A. japonica Nakai & H. Hara	sect. Villosae	Gehrke / BG-E 419 (ZH)	EU072631	EU072543
A. lapeyrousii Buser[2]	sect. Pubescentes	Gehrke / BG-E 494 (ZH)	EU072634	EU072546
A. longana Buser	sect. Coriaceae	Frost-Olsen / 11549 (ZH)	EU072635	EU072547
A. mollis (Buser) Rothm.	sect. Erectae	Gehrke / BG-E 420 (ZH)	EU072638	EU072550
A. montserratii S.E.Fröhner	sect. Ultravulgares	Lippert / 402 (ZH)	EU072639	EU072551
A. nitida Buser	sect. Glaciales	Lippert / 415 (ZH)	EU072640	-
A. oscensis S.E.Fröhner	sect. Pubescentes	Gehrke / BG-E 404 (ZH)	EU072641	EU072552
A. pentaphyllea L.[2]	sect. Pentaphylleae	Gehrke / BG-E 400 (ZH)	EU072643	EU072554
A. plicata Buser[2]	sect. Plicatae	Frost-Olsen / 11575 (ZH)	EU072644	EU072555
A. saxatilis Buser[2]	sect. Alpinaeser. Saxatiles	Frost-Olsen / 8088 (ZH)	EU072645	EU072559
A. schmidelyana Buser	sect. Plicatae	Gehrke / BG-E 391 (ZH)	EU072647	EU072561
A. splendens Christ[2]	sect. Splendentes	Frost-Olsen / 7587 (ZH)	EU072648	EU072563
A. subsericea Reut.	sect. Glaciales	Frost-Olsen / 11984 (ZH)	EU072651	EU072566
A. tenerifolia S.E.Fröhner	sect. Alchemilla	Frost-Olsen / 407 (ZH)	EU072652	EU072567
A. tenuis Buser	sect. Decumbentes	Frost-Olsen / 9716 (ZH)	EU072653	EU072568
A. transiens (Buser) Buser	sect. Alpinaeser. Saxatiles	Frost-Olsen / 12454 (ZH)	EU072654	EU072569
A. vetteri Buser	sect. Flabellatae	Frost-Olsen / 9097 (ZH)	EU072656	EU072571
A. vulgaris (syn. of *A. acutiloba*) Stev.[1]	sect. Alchemilla	Frost-Olsen / 460 (ZH)	EU072657	EU072573

***Aphanes* species**

Ap. arvensis L.[2]	sect. Quadridentatae	Rydberg / s.n. (S)	-	U90819
Ap. arvensis L.[2]	sect. Quadridentatae	Eriksson / s.n. (SBT)	AJ512234	-
Ap. cornucopioides Lag.	sect. Quadridentatae	J.Lambinon / 96/707 (M)	EU072660	EU072576
Ap. floribunda (Murb.) Rothm.	sect. Quadridentatae	R.Deschartes / 10292 (M)	EU072661	-
Ap. innexpectata W. Lippert	sect. Quadridentatae	Dörr / s.n. (M)	EU072662	EU072577
Ap. minutiflora (Azn.) S.Snogerup, Bothmer &	sect. Quadridentatae	Auguier / 1723 (M)	EU072663	EU072578

M.A.Gust.				
Ap. sp. Bolivia -	unknown	Beck / 4635 (LPB)	EU072664	EU072579
***Lachemilla* species**				
L. angustata Romol.	Described 1996, acc. to Romoleroux ser. Nivalis (sensu Romoleroux)	S.Laegard & I.Grignon / 19394 (QCA)	EU072666	EU072581
L. aphanoides (Mutis) Rothm.[2]	Sect. Aphanoides subsect. Glomerulatae, ser. Aphanoides	Romol. / 4110 (QCA)	EU072667	EU072582
L. diplophylla (Diels) Rothm.[2]	Sect. Diplophylla	E.Ternews & V.Rivera / 280 (QCA)	EU072668	EU072583
L. hispidula (Perry) Rothm.	Sect. Aphanoides subsect. Nivales, ser. Nivales	Romol. / 4119 (QCA)	EU072669	EU072584
L. holosericea (Perry) Rothm.	Sect. Aphanoides subsect. Subnivales, ser. Aphanoides	Romol. / 4118 (QCA)	EU072670	EU072585
L. mandoniana (Wedd.) Rothm.	Sect. Aphanoides subsect. Pachyrrhizae, ser. Pinnatae	Romol. / 4111 (QCA)	-	EU072586
L. mandoniana (Wedd.) Rothm.	Sect. Aphanoides subsect. Pachyrrhizae, ser. Pinnatae	P.Skelnar & V. Kosteckova / 66-2 (QCA)	EU072671	-
L. nivalis (Kunth) Rothm.	Sect. Aphanoides subsect. Nivales, ser. Nivales	Romol. / 4000 (MSB)	-	EU072587
L. orbiculata Rydb.	Sect. Aphanoides subsect. Radicantes; ser. Orbiculatae	Romol. / 4115 (QCA)	EU072672	EU072588
L. pectinata (Kunth) Rothm.	Sect. Aphanoides subsect. Radicantes, ser. Orbiculatae	K. Romoleroux / 4072 (QCA)	EU072673	-
L. pinnata (Ruiz. & Pav.) Rothm.	Sect. Aphanoides subsect. Pachyrrhizae, ser. Pinnatae	J.C.Solomon / 17431 (QCA)	EU072674	EU072589
L. rivulorum (Rothm.) Rothm.	Sect. Aphanoides subsect. Subnivales	P.Sklenar & V. Sklenardua / 2247 (QCA)	EU072675	-
L. rupestris (Kunth) Rothm.	Sect. Rupestres, ser. Aphanoides,	P.Sklenar & V.Sklenardua / 3033 (QCA)	EU072676	-
L. tanacetifolia Rothm.	Sect. Rupestres, descr. In 1935 acc. to Romoleroux ser. Pinnatae	P. Skelnar & V. Kostechova / 57-2 (QCA)	EU072677	EU072590
L. vulcanica Rydb.	Sect. Procumbentes, ser. Aphanoides	S. Laegaard / 17701 (QCA)	EU072678	-
L. vulcanica Rydb.	Sect. Procumbentes, ser. Aphanoides	Romol. / 4120 (QCA)	-	EU072591
Outgroup	**tribe/subtribe**			
Comarum palustre L.	Fragariinae	Gehrke/ BG-E412 (ZH)	EU072665	EU072580
Comarum salesovianum (Steph.) Aschers. & Graebn.	Fragariinae	Eriksson & Vretblad / TE751 (SBT)	AJ512228	AJ511779
Dasiphora fructicosa (L.) Rydb.	Fragariinae	Karlsson / 94074 (LD)	AF348557	U90809
Fragaria viridis Weston	Fragariinae	CFRA / 333 (OR)	AF163550	AF163506
Potentilla reptans L.	Potentillinae	Eriksson / 650 (G)	-	U90784
Potentilla reptans L.	Potentillinae	Eriksson / 822 (SBT)	AJ512241	-
Potentilla stenophylla Diels	Potentillinae	Eriksson & Vretblad / TE763 (SBT)	AJ512240	AJ511780
Rosa majalis Herrm.	Roseae	Eriksson / 641 (GH)	AJ512229	U90801
Sibbaldia cuneata Hornem.	Fragariinae	Gehrke / BG-K413 (ZH)	EU072679	EU072592
Sibbaldia procumbens L.	Fragariinae	Gehrke / BG-S 397 (ZH)	EU072680	EU072593
Sibbaldianthe bifurca (L.)	Fragariinae	Karis / 412 (S)	-	PBU90786

Kurtto & T.Erikss.				
Sibbaldianthe bifurca (L.) Kurtto & T.Erikss.	Fragariinae	Eriksson / 811 (SBT)	**AJ512224**	-
Sibbaldiopsis tridentata (Aiton) Rydb.	Fragariinae	Hill / 17146 (A)	-	**PTU90791**
Sibbaldiopsis tridentata (Aiton) Rydb.	Fragariinae	Eriksson & Smedmark / 40 (SBT)	**AJ512236**	-

SUMMARY

In this thesis I have investigated the role of colonisation frequencies (chapter 1) and in situ diversification (chapter 2) in the African high mountains of Tropical and Southern Africa. I have focused on plant elements from temperate areas and have mainly concentrated on three genera, i.e. ladies mantle (*Alchemilla;* Rosaceae), sedges (*Carex;* Cyperaceae) and buttercups (*Ranunculus;* Ranunculaceae). To do this I have reconstructed phylogenetic hypotheses of all three groups based on DNA sequence data (*Carex* and *Ranunculus* in chapter 1, *Alchemilla* in chapter 3) and produced a taxonomic synopsis of *Carex* in sub-Saharan Africa and Madagascar (chapter 4).

Chapter 1:

Chapter 1 concerns colonisation frequency and the Northern Hemisphere origin of pan-temperate plant elements in the African high mountains

In this chapter I show that the pan-temperate floral elements *Alchemilla, Carex* and *Ranunculus* have colonised the African high mountains several times. I investigated this by reconstructing a hypothesis of their phylogenetic relationships. I used parametric and non-parametric bootstrapping methods too tested the monophyly of the African mountain clades plus their monophyly with at least one additional sister species, from outside this area. I demonstrate that *Carex* colonised the African high mountains at least twelve times, while *Ranunculus* arrived and established itself at least four to six times. That *Alchemilla* arrived only twice is derived from chapter 3. Further investigation of the source areas of these colonisations, using ancestral area reconstructions and allowing for topological uncertainty, show that all three taxa are of temperate Northern Hemisphere, i.e. Holarctic, origin. The results also demonstrate that there is little evidence for recruitment from Africa to other areas.

Chapter 2:

In Chapter 2 the diversification of the pan-temperate plant lineages on the African high mountains are investigated.

The African lineages in *Carex* and *Ranunculus,* which I showed in chapter 1 to have colonised the African high mountains several times, have undergone varying amounts of in situ speciation. In chapter 2 I investigated what were the main factors influencing this diversification. I employ the unusual approach of investigating the repetitive recruitments of *Carex* and *Ranunculus* into the temperate climate zones of the African mountains. We use generalised linear models (GLM) under a quasipoisson distribution to test the response of different clade size estimations on the predictive models incorporating one or more important abiotic factors such as distribution range, distance from ancestral area, altitudinal range, number of vegetation zones, number of habitat types, light requirement, water availability and habitat heterogeneity. We can show that clade size shows a positive

response with a high explanatory power to a combined model including age, distribution and habitat, as represented by water availability. This means that pan-temperate plant lineages in the African high mountains which have only a few species are likely to be too young and too restricted in their distribution and habitat range to have diversified in Africa.

Chapter 3:

In chapter 3 a molecular phylogenetic reconstruction of ladies mantle is presented.

Chapter 3 concerns the closely allied genera *Alchemilla, Aphanes* and *Lachemilla*, which have been treated by various authors at different taxomomic levels. They have been either including as different genera in a single tribe, the Alchemillinae, or as subgenera in a single genus, *Alchemilla*. We reconstructed a phylogenetic hypothesis for this group for the first time and show that whilst all three genera form a monophyletic group. Two of the three genera (*Aphanes* and *Lachemilla*) are themselves are monophyletic, one (*Alchemilla*) is not. We identified a clade including all the African species of *Alchemilla*, which we called the Afromilla-clade. This result was in part unexpected: *Alchemilla, Aphanes* and *Lachemilla* were believed to from a natural group, but it has never before been hypothesised that African *Alchemilla* is monophyletic. We therefore suggest treating *Alchemilla, Aphanes* and *Lachemilla* as a single genus *Alchemilla*, based on three criteria: Monophyly, the lack of evident morphological characters for the identification and description of the Afromilla-clade at the rank of genus (without which *Alchemilla* from Eurasia would be rendered paraphyletic) and nomenclatural stability.

Chapter 4:

A synopsis of sedges (*Carex*) in sub-Saharan Africa and Madagascar is presented in chapter 4.

The last chapter comprises an α-taxonomic treatment: a synopsis of *Carex* in sub-Saharan Africa and Madagascar. It provides a key, synonymy, habitat descriptions, and distributions for the 84 species and an additional five infraspecific taxa. The genus *Carex* comprises c. 1600-2000 species, making it one of the largest genera of vascular plants. The last comprehensive treatment of *Carex* in Africa dates back to Kükenthal's monograph of the subtribe Cariceae in 1909. Subsequent descriptions of new taxa and regional taxonomic treatments have led to inconsistencies in species delimitations and confusion regarding the identification of specimens and correct application of names. The synopsis presented here is intended to summarise the scattered literature on *Carex* in Africa, including notes on the taxonomic status of species as appropriate and a comprehensive key for all species of *Carex* from Tropical and Southern Africa and Madagascar.

ZUSAMMENFASSUNG

In der vorliegenden Doktorarbeit untersuche ich the Rolle von Kolonisationen (Kapiel 1) und *in situ* Diversifikationen (Kapitel 2) in den Afrikanischen Hochgebirgen des Tropischen- und Südlichen- Afrikas. Ich konzentriene mich dabei auf die Pflanzenelements des temperaten Regionen und habe mich auf drei Gattungen beschränkt, d.h. der Frauenmantal (*Alchemilla,* Rosaceae), Seggen (*Carex*, *Cyperaceae)* und Butterblumen (*Ranunculus*, Ranunculaceae). Um dies zu erreichen habe ich für alle drei Gruppen eine molekularphylogenetische Rekonstruktion erstellt (siehe für *Carex* und *Ranunculus* Kapitel 1, für *Alchemilla* Kapitel 3). Außerdem habe ich für *Carex* im subsaharischen Afrika und Madagaskar eine α-Taxonomische Synopse erarbeitet (Kapitel 4).

Kapitel 1:

Im ersten Kapitel geht es um die Besiedlungshäufigkeit und die nordhemisphärische Herkunft der pan-temperate Pflanzenelemente in den Afrikanischen Hochgebirgen.

Ich zeige im ersten Kaptiel, dass die pan-temperaten Florenelemente *Alchemilla, Carex u*nd *Ranunculus* die Afrikanischen Hochgebirge mehrmal besiedelt haben. Dies habe ich durch die Erstellung einer Rekonstruktionshypothese der phlyogenetischen Verwandschaftsverhältnisse dieser Gruppen. Ich habe parametrische und nicht-parametrische Bootstrappmethoden verwendet, um die Monophlie der Afrikanischen Hochgebirgsgruppen und ihre Monophlie mit zumindest einer zusätzlichen Art, die nicht aus dem Untersuchungsgebiet kommt, zu testen. Ich kann zeigen, dass *Carex* die Afrikanischen Hochgebirge mindestens zwölf mal besiedelt hat, währned *Ranunculus* mindestens vier bis sechmal angekommen ist und sich etabliert hat. Die Tatsache, dass *Alchemilla* nur zweimal angekommen ist wird im Kapitel 3 gezeigt. Die weitere Untersuchung der Herkunftgebiete dieser Besiedlungen durch „Ancestral Area Reconstructions“ unter Berücksichtigug topologischer Ungewissheit zeigt, dass alle drei Gruppen aus den temperaten Gebieten der Nordhemispähre stammen, d.h. Holarktisch sind. Die Ergebisse zeigen ausserdem, dass des wenig Hinweise für die eine Besiedlung anderer Gebiete von Afrika her.

Kapitel 2:

Das Kapitel 2 beschreibt die Diversifikation der pan-temperate Pflenzenelemente *Carex* und *Ranunculus* auf den Hochafrikanischen Gebirgen.

Die Afrikanischen Pflanzengruppen *Carex* und *Ranunculus*, von denene ich im Kapitel 1 zeigen konnte, dass sie die Afrikanischen Hochgebirge mehrere male besiedelt haben, haben dort unterschiedliche Mengen an Artbildung durchgemacht. Im Kapitel 2 beschäftige ich mich mit den Faktoren, welche diese Artbildung beeinflusst haben könnte.

Ich verwende dazu den ungewöhnlichen Ansatz die wiederholten Siedlungsereignisse in *Carex* und *Ranunculus* in der temperate Klimazone der Afrikscniaschen Berge zu untersuchen. Ich tue dies durch die Verwendung von Generalisierten Linearen Modellen (GLM) mit einer Quasipoisson-Verteilung um die Bedeutung verschiedener Faktoren auf verschiedne Schätzunger der Grösse der Monophyla zu untersuchen. Die Modelle beinhalten dabei ein oder mehrere, wichtige (a-)biotische Faktoren wie Verbreitung, Abstand zum Herkunftsort, okkupierter Höhenbereich, Anzahl der Vegetationszonen, Anzahl der Habitattypen, Lichtbedarf und Habitatsheterogenität. Ich kann zeigen, dass die Grösse der Monophyla positive auf ein kombiniertes Model von Alter, Verbreitung und Habitat, vertreten durch Wasseranspruch und Höhenfaktoren, anspricht und zwar mit einer hohen Erklärungsstärke. Dies Bedeutet, dass die pan-temperaten Pflanzenelemente in den Afrikanischen Höchgebirgen, die nur wenige Arten haben, wahrscheinlich zu jung und nicht weit genug Verbreitet sind, sowie eine zu enge ökologische Amplitude haben, um Artbildung in Afrika durchgemacht zu haben.

Kapitel 3:

Im 3. Kapitel wird eine molecularphylogenetische Rekonstruktion der Frauenmäntel präsentiert.

Das Kapitel 3 geht um die eng miteinander verwandten (Unter-)Gattungen *Alchemilla, Aphanes* and *Lachemilla*, die von verschiedenen Authoren auf unterschiedlichem taxonomischen Niveau behandelt woren sind. Sie sind entweder als getrennte Gattugen in einem Tribus, den Alchemillinae, angesehen worden oder als Untergattungen in einer einzigen Gattung, *Alchemilla*. Ich präsentiere hier für diese Gruppe zum ersten mal eine molecularphylogenetische Hypothese and zeige, dass alle drei Gattungen ein Monophylum bilden. Gleichzeitig sind zwei der drei Gattungen (*Aphanes* und *Lachemilla*) Monophyla, während eine (*Alchemilla*) dies nicht ist. Ich identifiziere ausserdem ein Monophylum, dass alle Afrikanischen Arten von *Alchemilla* einschliesst und das ich die Afromilla-Gruppe nenne. Dieses Ergebniss ist teilweise unverhergesehen, da zwar angenommen wurde, dass *Alchemilla, Aphanes* und *Lachemilla* natürliche Gruppen darstellen, aber es bisher noch nie angenommen wurde, dass die afrikanischen *Alchemillen* ein Monophylum bilden. Ich schlage daher vor *Alchemilla, Aphanes* und *Lachemilla* als eine einzige Gattung *Alchemilla* anzuerkennen und zwar basierend auf drei Kriterien: Die Monophylie, das Fehlen von hervortretenden morphologischen Eigenschaften für die anerkennung und Beschreibung der Afromilla-Gruppe auf der Rangstufe einer Gattung (ohne dies *Alchemilla* paraphyletisch weren würde) und nomenglatorischer Stabilität.

Kapitel 4:

Eine Synopse von *Carex* (Seggen) im subsaharischen Afrika sowie Madagaskar eir in Kapitel 4 vorgestellt.

Das letzten Kapitel, Kapitel 4, besteht aus einer α-taxonomischen Abhandlung, einer Synopse von *Carex* aus dem tropischen und südlichen Afrika, sowie Madagaskar. Sie beinhaltet Schlüssel, Synonymie, Habitatbeschreibungen und Verbreitungsdaten von 84 Arten und zusätzlichen fünf Unterarten. Die Gattung genus *Carex* (Cyperaceae; Cariceae) umfasst etwa 1600-2000Arten, was sie zu einer der grössten Gattungen von Gefässpflanzen weltweit macht. Die letzte umfassende Bearbeitung von Carex in Afrika ist Bestandteil der Monographie des Untertribus Cariceae von Kükenthal aus dem Jahre 1909. Spätere Beschreibungen neuer Arten und regionale Bearbeitungen haben zu unbeständigen Artbeabgrenzungen und Irreführungen in Bezug auf Identifikationen und der richtigen Anwendung von Namen geführt. Diese Synopsis soll die verstreuten Informationen verschiedener Literatur über Carex in Afrika zusammenbringen und beinhaltet, wenn angebracht, Notizen über den taxonomischen Status von Arten, sowie umfassende Schlüssel zu allen Carex Arten im subsaharischen Afrika und Madagaskar.